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THE CONDOR

VOLUME 59 NOVEMBER-DECEMBER, 1957 NUMBER 6

THE CAVE SWALLOW IN TEXAS

By ROBERT K. SELANDER and JAMES KENNETH BAKER

Among the group of birds of tropical and subtropical distribution that reach their northern limits in the southwestern United States, the Cave Swallow (*Petrochelidon fulva*) is of special interest since it nests colonially in caves. It was first reported in the United States by Scott (1890), who collected two vagrants of the Cuban and Isle of Pines race, *P. f. "cavicola"* (= *coronata, fide* Hellmayr, 1934:34), on Garden Key, Dry Tortugas, Florida, on March 22 and 25, 1890. Twenty years later Bishop (1910:479) reported specimens obtained in Kerrville, Kerr County, Texas, which he referred to *P. f. pallida,* a race described by Nelson (1902:211) from Saltillo, Coahuila, México. That the Cave Swallow breeds in Texas was established in 1915 by Thayer's report of nests and eggs collected near Japonica, Kerr County. A year later the existence of "several isolated colonies" six miles west of Ingram, Kerr County, was announced by Smith (1916:191). Recently an extension of known breeding range to Eddy County, New Mexico, was reported (Kincaid and Prasil, 1956:452), and the existence of a colony in Edwards County, Texas, was briefly noted (Wolfe, 1956:50, and Pettingill, 1957:32). With the exception of these reports, a record of two individuals seen on the Tortugas in June, 1915 (Hull, 1939:24), and a description of a ceratophyllid flea from nests in Uvalde County, Texas (Eads, 1956:73–76), no further accounts of the Cave Swallow in the United States have been forthcoming in the 41 years since Smith's report. It therefore seems desirable to present additional information concerning variation, distribution, and ecology of this species in Texas.

ACKNOWLEDGMENTS

We are indebted to Dr. Richard B. Davis, Research Associate, Johns Hopkins University, Dr. Richard B. Eads of the Texas State Department of Health, and Colonel L. R. Wolfe of Kerrville for data on distribution and status in Texas and to Mr. William Hettler, Mr. David Kyser, Mr. Fred Berner, and several other members of the University of Texas Speleological Society for information on caves and for assistance in our investigations of them. Specimens in the United States National Museum and in the Museum of Comparative Zoology were made available on loan through the courtesy of Dr. Herbert Friedmann and Dr. Raymond A. Paynter, Jr., respectively. Tape recordings of calls were made by Mr. Wayne McAlister.

DISTRIBUTION

The Cave Swallow breeds in the Greater Antilles from Puerto Rico west to the Dominican Republic, Haiti, Jamaica, Cuba, and the Isle of Pines; the Cuban and Isle of Pines swallows are recognized as a separate race, *P. f. coronata.* On the continent the species breeds in Yucatán (*P. f. citata*) and in central Chiapas (subspecies?; see Amadon and Eckelberry, 1955:75) and, as *P. f. pallida,* in Eddy County, southeastern New Mexico, in central Texas, and in northeastern México, where it is known from three localities in Coahuila (Saltillo, Sabinas, Monclova) and one in Tamaulipas (Miqui-

huana). According to Hellmayr (1934:35) the Peruvian and Ecuadorian swallow *rufocollaris* is conspecific with *P. fulva*.

In Texas nesting of this colonial swallow is confined to limestone caves along the southern edge of the Edwards Plateau, a massive upland extending over much of the central and southwestern parts of the state. On the south and east the plateau descends to the low flatlands of Texas over the maturely eroded Balcones Escarpment, which decreases in height from 1500 feet at Del Rio near the Rio Grande to less than 100 feet north of Austin. Along the escarpment, where thick strata of limestone are exposed and highly dissected, numerous springs and caves occur, the latter ranging in size from small pits or shelters to gigantic cavern systems. Several of the larger springs are sources of rivers which flow to the lowlands.

The most widespread plant association of the dissected southern and southeastern parts of the plateau is a scrub forest of Mexican cedar (*Juniperus mexicana*), Texas oak (*Quercus texana*), and stunted live oak (*Quercus virginiana*). Extensive areas have been cleared and converted to grassland or savannah by cattle ranchers. The climate of this region is semiarid-mesothermal, with average annual potential evapotranspiration of 39.27 inches (Thornthwaite, 1948).

The distribution of breeding colonies of the Cave Swallow in Texas is shown in figure 1. Many, perhaps most, of the larger caves east of the Pecos River in western Val Verde County and west of Kerrville, Kerr County, are inhabited by these swallows.

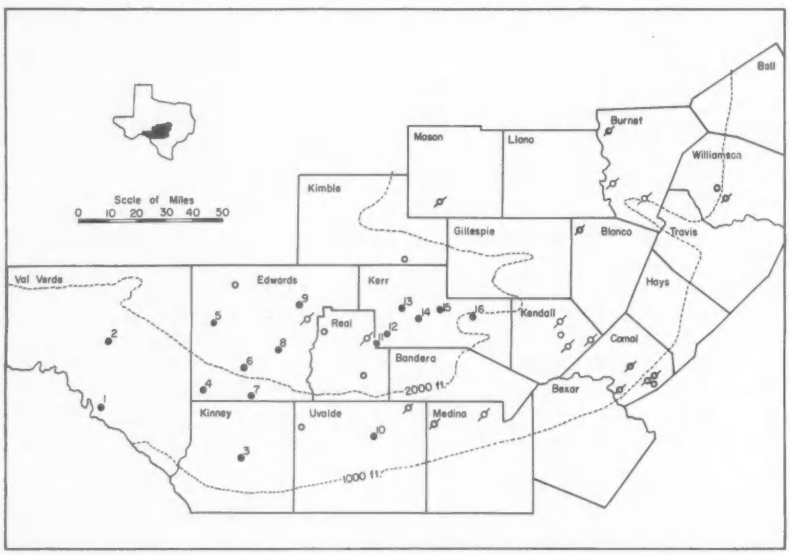

Fig. 1. Distribution of colonies of the Cave Swallow in Texas. Dots represent caves inhabited by swallows; circles with diagonal lines, seemingly suitable caves not occupied by swallows; circles, caves not investigated but judged as suitable from descriptions in the literature. 1. Abominable Sinkhole. 2. Fern Cave. 3. Webb Cave. 4. Rucker Bat Cave and Saltillo Cave. 5. Dunbar Cave. 6. Whitworth Ranch Cave. 7. Green and Hillcoate caves, Seargeant Ranch. 8. Thurman Cave. 9. Devil's Sinkhole. 10. Frio Cave. 11. Johnson Ranch Cave. 12. Wilson Cave. 13. Stower Cave. 14. Merritt Ranch caves. 15. 6 miles west of Ingram. 16. Kerrville.

South of the Balcones Escarpment, which follows a line drawn through central Kinney, Uvalde, and Medina counties, no caves of any size are found; and north of Val Verde, Edwards, and Kerr counties swallows have not been recorded although several caves are present in that part of the plateau. Undoubtedly other colonies will be discovered in Texas, but it seems rather unlikely that the breeding range extends much farther east or north than indicated by the distribution of colonies shown in figure 1. The most curious feature of the distribution of this swallow is that it occurs no farther east than Kerrville, since seemingly suitable caves are found in Bexar and other counties along the eastern margin of the Edwards Plateau east of Kerr County.

Special environmental requirements for nesting of the Cave Swallow in Texas include (1) a cave providing rather extensive roughened or, preferably, pitted surfaces for attachment of nests *within the twilight zone* and at least four feet above the floor; and (2) a source of water for drinking and of mud or mud substitute (guano) for nest building either within the cave itself, in which case colonies may inhabit caves far removed from surface water, or within foraging range, which extends only a few miles from the cave. Water for mud may be provided either by seepage within the cave or by run-in surface water. Swallows regularly visit ranchers' open water tanks (ponds) to drink and in some instances to obtain mud. Undoubtedly these man-made water sources have been important in permitting the swallows to continue breeding in recent years within the drought-stricken central Texas region, where naturally occurring surface water was practically non-existent over extensive areas, except for a few days each year following rains. As a result of its ability to utilize cave walls for nesting and because in certain situations it may be independent of surface water, the Cave Swallow is able to maintain breeding colonies in arid regions which are uninhabitable to the Cliff Swallow (*Petrochelidon pyrrhonota*). The latter species requires for nesting a protected overhanging cliff or cliff substitute in close proximity to a source of mud (Emlen, 1952:196) and, at least in Texas, an extensive meadow, lake, or flood plain over which to forage.

Within the breeding range of the Cave Swallow in Texas the Cliff Swallow (*P. p. tachina*) also occurs, nesting on limestone cliffs along the major streams. Some of the largest colonies of the Cliff Swallow in Texas are in Kerr County along the North Fork of the Guadalupe River, for example at Camp Stewart (= Japonica) and at a lake along the river six miles west of Camp Stewart, and at Prade Ranch, in Real County along the Frio River. Contact between the two species of swallows in Texas is probably an uncommon occurrence as a result of their differing ecologic distributions. We have no record of the two species associating. The Cave Swallow also is sympatric with the race *P. p. melanogaster* of the Cliff Swallow in Coahuila, as at Saltillo (Burleigh and Lowery, 1942).

THE BREEDING COLONIES

The following is an account of all caves in Texas known by us to be inhabited by Cave Swallows. Several of the caves listed are also mentioned by White (1948) in his article on the caves of central Texas.

EDWARDS COUNTY. *Devil's Sinkhole, 10 miles northeast of Rocksprings.*—This giant cave, the largest of its type in the United States, has a sink-type opening 60 feet in diameter, which drops 110 feet vertically and widens into a large chamber partly filled by a conical mound of rock breakdown 100 feet in height. Swallows nest on the slanting roof of the lower chamber 110 or more feet below ground level and high above the sides of the rock mound.

A source of mud for nests is provided by water which seeps from the sides of the sink, wetting soil that has accumulated on the narrow limestone ledges and dripping to

the mound of rock and guano below. Brown Towhees (*Pipilo fuscus*) and Tufted Titmice (*Parus bicolor*) were seen to enter the sinkhole and forage over moss and lichens on the lower ledge of the sink about 100 feet below ground level. A Canyon Wren (*Catherpes mexicanus*), presumably a resident in the sink, foraged on ledges 70 feet down. Horned Owls (*Bubo virginianus*) also nest on ledges in the sink.

On the morning of September 21, 1956, first indication that swallows were preparing to leave the cave was a chorus of chattering calls at 6:10 a.m., given by birds in

Fig. 2. Entrance to Dunbar Cave, Edwards County. Xeric vegetation shown in background is typical of this part of the Edwards Plateau.

the lower chamber before they entered the sink but clearly audible from ground level. Shortly thereafter a compact flock of about 100 birds appeared at the base of the sink, executed three rapid ascending spirals, and emerged from the entrance in close formation, flying at high speed and calling continuously. Other groups of from 25 to 100 birds followed until an estimated total of 500 birds had emerged. Invariably flights were preceded by loud choruses of calls, which continued during ascent. In loose formation the flocks circled high in the air above the cave and flew toward the east. At 7:30 a.m. a loose flock of several hundred swallows appeared high above the cave and descended to the entrance in slow spirals. At one point in their descent the birds suddenly gathered together in a compact flock as a female Sparrow Hawk (*Falco sparverius*) passed below them, only to separate again when the hawk had passed. As the circling flock passed a few feet above the entrance, a few individuals dove into the sink; then suddenly the

whole flock dropped in. Some birds spiraled down the sink while others dove straight down. Many birds left the cave between 8:10 and 8:15 a.m. and again flew eastward. Emerging groups spiraled clockwise and counter-clockwise in the sink with about equal regularity; ascent of the sink always involved at least three full spirals, but some groups performed as many as 20.

Dunbar Cave, 21 miles west of Rocksprings.—The entrance of this cave is a vertical sink about seven feet in diameter (fig. 2), which penetrates 15 feet of limestone

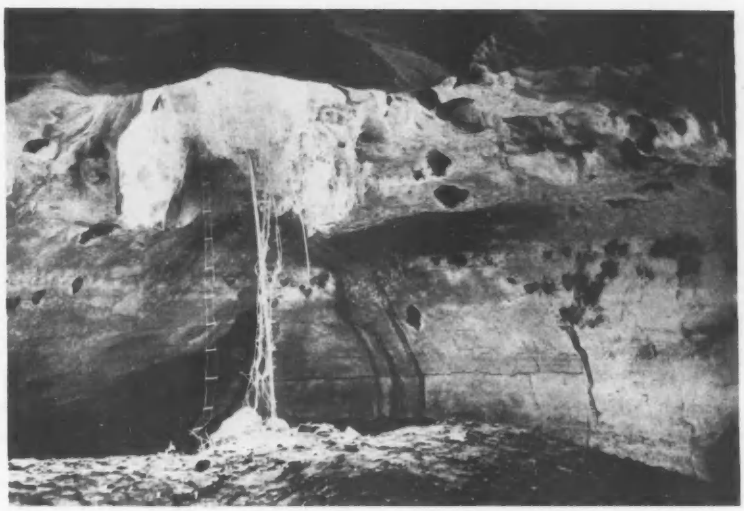

Fig. 3. First chamber of Dunbar Cave, Edwards County, taken from floor 30 feet below ground level. Note Cave Swallow nests in eroded pockets in the roof and on the walls.

before opening into an oval chamber approximately 70 feet in diameter and 15 feet in height. On the east and west sides of this chamber, passageways lead to other chambers of equal or larger size. About 400 swallows were present on September 29, 1956, perched on the 250-odd nests in the cave. All of these nests were located in the first chamber (see fig. 3). The greatest concentration of nests occurred on walls near the entrance sink, but a few were located up to 90 feet from the entrance. None was placed in the entrance shaft itself, which was exposed to direct sunlight.

In Dunbar Cave water seeping from the walls of the sink falls to the guano-covered floor of the first chamber, supplying a source of mud for the colony. Guano is produced by large numbers of cave bats (*Myotis velifer*) roosting in the cave, mainly in chambers other than the first, and by the swallows themselves.

At about 8 p.m. on September 29, all but 40 or 50 of an estimated population of 400 swallows left the cave when members of the University of Texas Speleological Society entered. The disturbed birds spent the night outside the cave, returning in a flock at 6:30 a.m. the next day. About 50 birds entered but after circling for an hour the majority was again driven away by our activities in and near the cave. Our presence in the cave greatly disturbed the birds, which began calling loudly and circled for several minutes in close formation and at high speed, just below the entrance, before flying out.

Rucker Bat Cave and Saltillo Cave, 35 miles southwest of Rocksprings.—On September 30, 1956, we found nests in crevices and pits in the roof of Bat Cave on the Rucker Ranch. This cave receives its name from the large numbers of Mexican free-tailed bats (*Tadarida mexicana*) which roost in a chamber at the rear of the large main room. The main chamber is about 100 feet wide, several hundred feet long, and 50 to 60 feet in height. It opens to the surface through a large arched entrance; all of the main chamber is within the twilight zone and much of it is rather well illuminated. No birds were present on the day of our visit but to judge from numbers of nests seen, the colony is smaller than those at Dunbar Cave and the Devil's Sinkhole.

There is evidence that considerable volumes of water accumulate in the cave following rains; possibly the swallows obtain mud within the cave.

Saltillo Cave is on the Rucker Ranch a few miles from Bat Cave. It opens through a sink about 8 feet in diameter which penetrates limestone for about 5 feet to open in the ceiling of a large chamber having a floor 45 feet below ground level. Twilight zone illumination prevails throughout the cave. On December 2, 1956, Baker estimated that 1500 nests were located in the cave, mostly on the walls of three domes in the ceiling about 40 feet above the floor, and on April 7, 1957, between 2500 and 3000 swallows were present. In all probability this is the largest breeding colony of Cave Swallows in this country. On the cave floor beneath the domes, piles of bird guano up to 5 feet in height have accumulated. One row of about 10 nests apparently had been vandalized by a predator, possibly a ring-tailed cat (*Bassariscus astutus*), which had gained access to them by scaling the wall. The lowest nests in the cave were about 10 feet above the floor.

Whitworth Ranch Cave, 20 miles south-southwest of Rocksprings.—A colony of swallows is reported to inhabit a big shelter cave on the Whitworth Ranch, within 200 yards of Dragool Cave. Hettler found 400 birds there in August, 1956.

Thurman Ranch Cave, 15 to 20 miles south of Rocksprings.—On November 24, 1956, Kyser found approximately 50 nests in pits in the roof of this cave, which opens through three sinkholes measuring from 4 to 12 feet in diameter and penetrating 6 feet of limestone. Nests were located in the entrance room, a chamber 10 feet high and about 15 feet wide; the lowest nest was only 4 feet above the floor.

Hillcoate Cave and Green Cave, Seargeant Ranch on Rocksprings-Bracketville Road near Kinney-Edwards county line.—Hillcoate Cave opens through an arch 5 feet high and 15 feet wide in the side of a hill. The first chamber is 50 feet high, 100 feet wide, and about 500 feet long. About 50 Cave Swallow nests were seen by Baker on January 30, 1957, all of which were in the twilight zone within 100 feet of the entrance. The presence of nests of the Cave Swallow in Hillcoate Cave was first reported to us by Kyser, who explored the cave in November, 1956.

Green Cave is about one mile from Hillcoate Cave and is similar to it in dimensions. Baker noted about 50 nests there on January 30, 1957. Both caves on the Seargeant Ranch are within a mile of the ranch house, where windmill water tanks are located.

KINNEY COUNTY. *Webb Cave, Shahan Ranch, 7 miles north of Bracketville.*—This cave is entered by four sinks, the largest of which is 10 feet in diameter; these penetrate 20 feet of limestone to open into a chamber 30 feet in height. Kyser counted 150 nests in the cave on December 30, 1956. Water dripping from a hole in the ceiling near the entrance forms mud on the floor of the chamber, but several nests examined by Kyser were composed of mud which he judged to have been obtained outside the cave.

UVALDE COUNTY. *Frio Cave, Annendale Ranch, 7 miles south of Concan.*—This cave, one of the largest in Texas, consists of three large and two small chambers. Swallows nest on the pitted walls of the oval entrance room which is about 300 by 600 feet in

dimensions. Most of the entrance chamber is well lighted by way of two 20-foot chimneys and three arched entrances, total darkness being reached only in the inner 100 feet (White, 1948:61). Great hordes of Mexican free-tailed bats roost in the inner chambers.

VAL VERDE COUNTY. *The Abominable Sink, Ab Rose Ranch ("Old Mayfield Ranch"), 15 miles south of Comstock.*—A circular entrance sink about 35 feet in diameter penetrates 130 feet of conglomerate and shale to widen into an extensive chamber in limestone, which is in part filled with breakdown from the sinkhole. Apparently neither swallows nor bats inhabit the cave at the present time but on January 29, 1957, Baker found remnants of six or eight nests under a slab of shale about 120 feet down in the sink. There is evidence that the sink connecting the limestone chamber with the surface is still enlarging, as Mr. Rose reported that new breakdown had accumulated since his last visit. Possibly other nests were destroyed and the colony abandoned when this recent breakdown of the sink occurred.

Fern Cave, Martin Rose Ranch, 20 miles north of Comstock.—Fern Cave opens through a sink 25 feet in diameter and about 50 feet deep. In a chamber adjoining the entrance approximately 100 nests were found by Baker on January 29, 1957, most of which were on the sides of three large domes in the ceiling; a few nests were placed on walls about 20 feet above the floor of the cave. There is a water tank 200 feet from the cave entrance.

KERR COUNTY. *Cave near Japonica (= Camp Stewart).*—A nesting colony was found in June, 1914, by F. B. Armstrong (Thayer, 1915:102–103). Judging from the description quoted by Thayer, this cave is similar to the first chamber of Dunbar Cave described elsewhere. The entrance sink is about eight feet in diameter; ten feet down it widens into a "spacious chamber," the floor of which is 50 feet below ground level.

Six miles west of Ingram.—Smith (1916:191) reported "several isolated colonies" in this area, but unfortunately he failed to describe any of the caves or to fix their location more precisely.

Goat Shelter Cave and unnamed sinkhole, Johnson Ranch, 30 miles southwest of Hunt.—On October 9, 1956, we investigated two nesting sites at this locality reported to us by Eads. We found 80 nests in the Goat Shelter, a cave having an oval entrance 35 feet wide which opens obliquely down into a single chamber about 50 feet in diameter and 30 feet in height. Most of the nests were placed on the back wall and on the sides of large crevices and pockets in the roof. One nest was in an eroded pocket only 4½ feet above the cave floor. Another was only 15 feet in from the top of the entrance arch, in a well lighted part of the cave.

The second cave on the Johnson Ranch in which swallows nest is an unnamed sinkhole with a vertical entrance about 5 feet in diameter. A nest within the cave was visible from the ground surface. About 20 feet down the sink reportedly opens into a large chamber; we did not investigate the cave further.

A third cave on the ranch, a single dry chamber 10 feet in diameter and 9 feet in height, contained no nests. Apparently this cave is too small to furnish suitable nesting sites for a colony; also much of the wall surface is accessible to racoons (*Procyon lotor*) and other predators.

Wilson Cave, 20 miles southwest of Hunt.—This large shelter cave was visited on December 30, 1956. It contained perhaps 50 nests; all these were located in crevices and pockets in the walls and ceiling and so situated that direct sunlight did not fall on them. We were informed by the owners of the ranch that in the summer swallows regularly visit a water tank about two miles from the cave. Among specimens sent to us on loan from the U. S. National Museum is a female collected by B. E. Ludeman 20 miles southwest of Hunt on August 10, 1937.

Stower Cave, 13 miles west of Hunt.—Davis visited Stower Cave in the fall of 1956, finding a few nests. The cave is a sinkhole with an entrance 8 feet in diameter. No swallows were present when Berner visited the cave at noon on April 14, 1957.

R. R. Merritt Ranch Cave No. 1, 6 miles southwest of Hunt.—This cave is a single chamber 25 feet in diameter opening by way of an 8-foot circular sink 35 feet above the floor. On December 29, 1956, three nests were found under an overhanging ledge below the sink. Two other smaller caves on the Merritt Ranch are not inhabited by swallows.

Kerrville.—It is probable that specimens reported by Bishop (1910:459) as having been obtained at Kerrville were collected elsewhere than in the immediate vicinity of the town.

SEASONAL STATUS AND ANNUAL CYCLE

In Texas the Cave Swallow is a summer resident. Available data suggest that time of arrival at the nesting colonies in the spring varies markedly from year to year. According to a report by Pettingill (1957:32) the species arrives in Edwards County in April; in 1955 Eads (personal communication) noted that none was seen at Frio Cave, Uvalde County, on March 30, but on April 20 many birds were present. In 1957 swallows were present in large numbers at the Devil's Sinkhole and Webb and Frio caves as early as February 9; in 1915 Armstrong collected specimens at "Kerrville" on February 6, and large series were taken by him in late February and March.

A fresh egg found on the floor of Frio Cave on April 5, 1957, indicated that laying was under way, although none of the nests which we were able to examine contained eggs. At Dunbar Cave on April 7, 1957, building and repair of nests was almost completed, and the gonads of several specimens collected were in or were approaching breeding condition. One female had an ovary measuring 8 mm. in diameter and an enlarged oviduct; the mate of this bird had testes 11 mm. in length and a conspicuous cloacal protuberance (Salt, 1954). The testes of another male were 10 mm. long. Two other males had testes 3 and 5 mm. in diameter; probably the latter two are first-year birds. Their wing lengths are 106 and 109 mm., whereas wings of the two males with enlarged testes measure 111 and 112 mm. Also the coloration of the presumed first-year birds is relatively pale. All specimens collected on April 7 were extremely fat; the heaviest bird, a male, weighed 25.1 grams.

In May, 1955, eggs had been layed and a few young were hatched at Frio Cave (Eads, 1956:73). Armstrong took 43 eggs from nests in Kerr County on June 7 and 8, 1914, including two sets of three, eight sets of four, and one set of five (Bent, 1942:489). These facts suggest that two broods are raised. The eggs are similar to those of the Cliff Swallow, except for slight differences in shape suggested by data given by Bent (*loc. cit.*).

In 1956 fall migration took place or at least was completed sometime between September 30, when hundreds of swallows were present at Dunbar Cave, Edwards County, and October 9, when none was found at two nesting sites visited in Kerr County. In this period there was a sharp drop in nightly temperatures at Kerrville and in central Texas generally. On December 29 and 30, 1956, and January 29 and 30, 1957, swallows were not found at several nesting sites visited in Kerr, Val Verde, and Edwards counties. Several ranchers expressed belief that the Cave Swallow may be present throughout the winter, at least in small numbers; but other than the impressions of these individuals, we have no evidence of the occurrence of the species in Texas during November, December, and January. The winter range of the Texas population is unknown; possibly the birds move south only as far as northeastern México, but no information seems to be available as to whether or not Cave Swallows are present there in the winter months.

Both adult and juvenal Cave Swallows have a complete molt in the fall. The post-

nuptial molt is completed or nearly so prior to migration of the adults. Molt was under way in an adult female collected on August 10; primary 1 is new and 2 is one-half grown. All 15 adult specimens taken at the Devil's Sinkhole on September 21, 1956, are in advanced stages of molt, as indicated in table 1. We interpret the unusual degree of uniformity of molt stage in this sample as an expression of close synchrony of the annual cycle in members of a colony. Synchrony of nest building and laying and hatching dates in colonies of the Cliff Swallow is discussed by Emlen (1952).

Table 1

Molt Stages of Specimens of *Petrochelidon fulva pallida* Collected at Devil's Sinkhole, Edwards County, on September 21, 1956

Sex and age	Number of primaries molted						Number of secondaries molted						
	2	3	4	5	6	7	1	2	3	4	5	6	7
♂ ♂ adult				6	4	1					5	5	1
♀ ♀ adult				3	1						3	1	
♂ juv.			1					1					
? juv.	1						1						

Unexpectedly, only two of 25 specimens collected on September 21 and 30 are immature, as indicated by an unpillared cranium as well as by the fact that they still bear some juvenal feathers. Both immatures are well behind the adults in stage of molt (table 1). The age ratio of the sample is subject to several tentative interpretations, one of which is that immatures normally migrate or at least desert the colonies before the adults. Another possibility is that in 1956 the nesting efforts of the population of the Devil's Sinkhole (from which 18 of the 25 specimens were collected) and, perhaps, of that at Dunbar Cave were largely unsuccessful.

NEST STRUCTURE AND LOCATION

The form of the nest shell is shown in figure 4. It is a rounded half-cup similar to stages III or IV in construction of the familiar retort-shaped nest of the Cliff Swallow described by Emlen (1954:23–24). Wetmore and Swales (1931:321) reported that nests of *P. f. fulva* are sometimes enclosed above, with a small entrance in the side; but in none of the thousands of nests of *P. f. pallida* that we have examined was there any evidence of an attempt to roof over the nest by extending the walls of the cup. The wide range of variation in nest size shown in figure 4 is characteristic of most colonies visited. In large part it results from the use of nests in successive breeding seasons, the nests becoming progressively longer and wider as additional layers of pellets are added to the rim. The composition of pellets may vary from year to year, with the result that older nests often show three or four layers of different colors and textures (see fig. 4A). A small nest was 5.1 inches wide at the rim and 3.6 inches long; one of the larger nests examined was 7.2 inches wide and 6.2 inches long. Dimensions of most nests fall between these extremes. When thoroughly dry the large nest, including shell, lining, and a large quantity of detritus in the nest cavity, weighed 970 grams; the small nest weighed 268 grams. Presumably nests are occupied until the combined weight of the shell and the detritus within causes them to fall from the cave walls.

Although the size of pellets used in construction of the nest shell is similar in *P. fulva* and *P. pyrrhonota*, the walls are thicker in nests of the former species. In *P. fulva* the thickness (measured between protruding pellets) varies from 1.35 inches (range in 7 nests, 0.9–1.7) at the rim to 0.86 inches (range, 0.8–1.0) at the base. In *P. pyrrhonota* the thickness varies in different parts of the nest from 0.24 to 0.66 inches, with an aver-

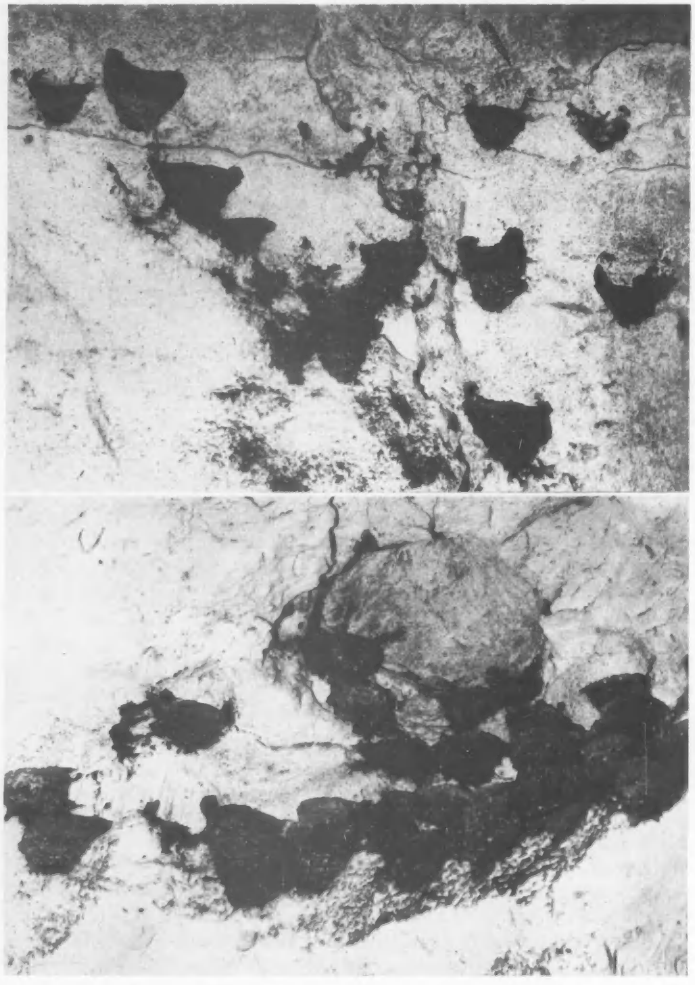

Fig. 4. Nesting sites of Cave Swallows in Dunbar Cave. Above, on vertical wall. Below, on sides of dome in roof; photograph taken looking up into dome.

age of about 0.44 inches (Emlen, 1954:21). Pellets from nests collected in Dunbar Cave are a mixture of weathered guano, soil, and limestone chips. Nest shells in some other colonies apparently are composed entirely of mud. The nest lining is a thin layer of cotton-like plant fibers of several types, thin strips of bark, fine grasses, and feathers. Much of the nest cup may be filled with a moist mixture of bat guano, old nest lining material, bits of eggshell, and fecal pellets of the myriads of insects and other arthropods

Fig. 5. Row of nests in eroded pockets up against ceiling in Dunbar Cave.

Fig. 6. Nest formed by partly sealing entrance of small pot-hole in limestone wall of Dunbar Cave.

which inhabit this mass of organic material; these include fleas, beetle larvae, and false scorpions. In Dunbar Cave, and presumably in other caves as well, the cave bat (*Myotis velifer*) frequently roosts on the roofs of pockets and crevices in which swallow nests are located and undoubtedly is a major contributor of guano. Probably it is the filling of the nest cup with guano and other organic material which necessitates extension of the rim by addition of new layers of pellets.

Emlen (1952:197) has presented considerable evidence to support his belief that the enclosed, retort-shaped nest of the Cliff Swallow "appears to be related to the intense localized territorialism of the species, the shell screening the nesting bird from its numerous close neighbors and thus enhancing social stability in the group." The enclosed top of the nest is regarded by Emlen as a late development in nest ontogeny in swallows, and, accordingly, he suggested that colonial nesting in *Petrochelidon* may have evolved recently.

The fact that the nest of the colonially nesting Cave Swallow is an unroofed structure can be reconciled with Emlen's views, provided location and spacing of nests in colonies are considered. It is certainly significant that in colonies of *P. fulva* we have never found large numbers of nests so closely grouped as in typical colonies of *P. pyrrhonota* (see for example, Emlen, *op. cit.*, fig. 7B). In most caves well over 50 per cent of the nests are located singly in small eroded pockets or crevices and are thereby effectively screened in all directions from neighboring nests. Irregularities in the surface of the cave walls determines spacing to some degree, preventing large concentration of nests in small areas, but the distribution of nests in all colonies visited clearly reflects a strong tendency for birds to build in isolated crevices and pockets or close up under an overhanging roof or ledge. Apparently flat vertical walls are used only when all other suitable

niches are occupied. Typical location of nests in eroded pockets is shown in figures 5 and 6; spacing of nests on a wall in Dunbar Cave is shown in figure 4. Figure 4 shows an unusually heavy concentration of nests on the sides of a large dome in the ceiling of this cave. Generally where two nests are in contact the upper one is a large nest that has been used for several years and the other, located below, is a small nest more recently built. It is unusual to find two nests in contact with the rims on the same level.

It is pertinent to this discussion of differences in nest structure in species of *Petrochelidon* to note that *P. fulva* nests in the twilight zone of caves, where illumination is relatively weak. From our observations, it seems probable that if *P. fulva* were to build nests having a roof and small tunnel entrance, it would have considerable difficulty in carrying out activities such as feeding the young within the nest and perhaps even in locating the nest entrance itself. Hence advantages resulting from the roofing of nests might well be outweighed by detrimental effects resulting from insufficient illumination in and about the nest.

Although in the United States the Cave Swallow nests only in caves, it is by no means so restricted in some other parts of its range. For example, in the Dominican Republic it has been found nesting not only in caves but also in clefts and crevices in cliffs, on ledges overhanging the sea, and on an iron bridge across a stream (Wetmore and Swales, 1931), situations typically selected by *P. pyrrhonota* in the United States. In Chiapas, México, Amadon and Eckelberry (1955:75–76) found *P. fulva* nesting beneath a portico along the plaza in Chiapa de Corzo and on the cathedral in Tuxtla Gutiérrez. We believe it is significant that both are regions in which *P. pyrrhonota* does not breed. The tentative inference is that where the two species are sympatric, as in Texas and New Mexico, nesting of *P. fulva* is restricted to caves by competition with *P. pyrrhonota*. Perhaps the superiority of the latter species stems in large part from its ability to establish larger colonies in limited areas of suitable nesting substrate, an ability dependent in turn, as suggested by Emlen, on the increased social stability resulting from the screening effect of the enclosed nests.

It is also of interest that in Trans-Pecos Texas, where the Cave Swallow apparently is absent, the Cliff Swallow occasionally nests in caves along rivers.

TAXONOMIC COMMENTS

There are no differences in color and pattern among specimens from Coahuila, Texas, and New Mexico that cannot be accounted for on the basis of individual or seasonal variation. Measurements of samples from these regions are presented in table 2; for comparison size data for *P. f. fulva* and *P. p. tachina* have been included. The large size claimed for *P. f. pallida* by Nelson (1902:211) and Ridgway (1904:56) on the basis of six specimens is confirmed by our large series. In color *P. f. pallida* differs from *P. f. fulva* in having the rufous pigments yellower (less reddish) and paler (less intense), especially on the rump, anterior under parts, flanks, and under tail coverts; centrally the under tail coverts are brownish gray rather than brown. Nelson (*loc. cit.*) probably got the erroneous impression that the reddish wash "is usually absent along sides of breast and body" in *P. f. pallida* from comparing his worn breeding specimens with fresher-plumaged material of *P. f. fulva*. In the fresh fall series from Texas all specimens show a conspicuous cinnamon wash in these areas, although the color is paler (near 7.5 YR 6/5, Munsell Book of Color) and less extensively distributed on the flanks than in *P. f. fulva*. With wear this wash is lost and the gray and dusky brown bases of the feathers of the flanks and breast are exposed, as in Nelson's material from Coahuila and Tamaulipas and in March and June specimens from Texas.

Weights of *P. f. pallida* derived from extremely fat specimens taken on September 21

were: ♂♂ 20.32 (18.4–22.3); ♀♀ 20.55 (20.0–21.1). On September 30 seven specimens were captured and held in captivity without food and water for 36 hours. When sacrificed, they showed little or no subcutaneous fat and averaged 17.1 grams (range, 17.4–18.4), showing an average weight loss of 2.7 grams.

Remnants of dark throat patch in P. fulva.—In 17 (34 per cent) of the 50 specimens of *P. f. pallida* examined, from one to seven feathers of the throat and/or anterior part of the breast have a terminal blackish brown mark, duplicating in shape and posi-

Table 2

Average and Extreme Measurements of *Petrochelidon* in Millimeters

	Sex	No.	Wing	Tail	Bill from base	Tarsus
P. f. pallida						
Texas	♂	13–23[1]	109.0 (106–112)	48.42 (47.0–49.9)	8.25 (7.6–8.7)	12.46 (12.1–13.0)
	♀	9	108.7 (104–113)	48.94 (47.8–50.7)	8.19 (7.5–8.5)	12.79 (12.3–13.6)
New Mexico	♂+?	3	110.9 (109–112)	49.57 (48.9–50.8)	8.60 (8.5–8.7)	12.57 (12.0–12.8)
Coahuila[2]	♂	1	107	48	.....	12
	♀	5	107.9 (106–110)	48.6 (47.0–49.5)	.....	12.1 (12.0–12.5)
P. f. fulva[3]						
Hispaniola	♂	8	99.5 (97–103)	41.6 (37.0–44.2)	7.9 (7.4–8.3)	12.5 (11.3–14.7)
	♀	2	100.5 (100–101)	43.4 (41.5–45.3)	7.9 (7.4–8.3)	12.5 (11.3–14.7)
P. p. tachina						
Texas	♂	18	104.0 (100–107)	46.89 (44.6–49.3)	7.55 (7.2–8.2)	11.81 (11.4–12.4)
	♀	9	102.9 (100–105)	46.39 (44.8–49.2)	7.61 (7.0–8.1)	11.60 (11.2–12.1)

[1] 13 specimens for wing and tail.
[2] Measurements from Ridgway (1904).
[3] Measurements from Wetmore and Swales (1931).

tion those which form the posterior part of the conspicuous metallic black throat and breast patch in *P. pyrrhonota*. In one female (Texas Nat. Hist. Collection 1264) these markings are very prominent, forming a patch 8 millimeters in diameter centrally on the breast and throat. In the majority of specimens of *P. f. pallida* these markings are entirely absent.

Because neither Ridgway (1904) nor other authors have noted the presence of throat markings in *P. fulva*, it was at first thought that their presence in specimens of *P. f. pallida* indicated hybridization with *P. p. tachina*. However, after examining large series of both *P. f. pallida* and *P. p. tachina* from central Texas and a small series of *P. fulva* from the Greater Antilles, we now favor a different interpretation.

Both in *P. f. pallida* and, to a lesser degree, in *P. p. tachina*, the size of the throat patch varies individually. By arranging four selected reference specimens of each of the two species in order of increasing size and conspicuousness of the throat patch, it was possible to demonstrate a gradual transition from the typical unmarked condition in *P. f. pallida* (class 0) to the extreme condition in *P. p. tachina* (class 7), in which the throat and anterior breast are almost solid glossy black (see fig. 7). Individual variation in *P. p. tachina* and in samples of *P. f. pallida* is shown in table 2, based on class scores assigned to adult and first-year specimens. There appears to be no sexual variation in this character, although larger samples might reveal slight but statistically significant differences. That relatively more specimens of *P. f. pallida* show throat markings in the sample of September, 1956, than in the sample taken in March and June, 1914, is doubtless attributable to the fact that the September birds are in very fresh plumage, whereas the others are in moderately worn plumage, which is, in most cases, badly

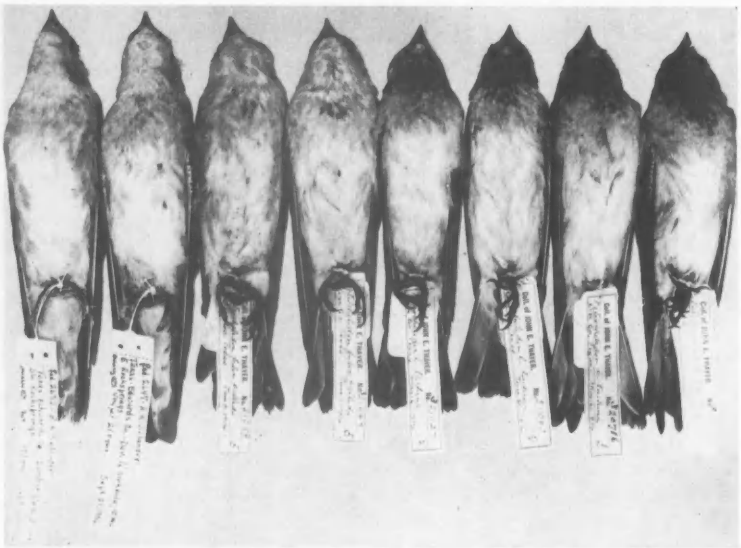

Fig. 7. Variation in throat pattern in Cave Swallows and Cliff Swallows. From left to right, four specimens of *Petrochelidon fulva pallida* (classes 0 to 3) and four of *Petrochelidon pyrrhonota tachina* (classes 4 to 7).

grease-stained and discolored. For this reason, in specimens collected in 1914, the markings are less conspicuous, especially in those having only a few small ones.

In order to investigate further the possibility that variation in throat pattern results from introgressive hybridization, we drew scatter diagrams to test for correlations between throat pattern and some other characters in which the two species differ. If recent hybridization were involved, correlation of intermediacy of characters would be expected in the presumed hybrids (Anderson, 1949). Evidence of correlation with throat pattern was found only for wing length in *P. f. pallida*; it was absent in both species in our comparisons of throat pattern versus (1) color of the forehead, (2) width of the forehead crescent, (3) color of the sides of the throat and chin, (4) color of the rump, (5) bill length, and (6) tarsal length. No intergradation between the species was noted in characters 1 through 3, but some overlap in color of the rump and in size occurs. The scatter diagram in figure 8 shows a weak correlation between wing length and throat pattern in male specimens of *P. f. pallida*, but not in *P. p. tachina*, and the absence of correlation in specimens of either species as regards throat pattern and tarsal length.

In *P. f. pallida* correlation between throat pattern and wing length shown in figure 8 would be expected if throat markings were more prevalent and the wing averaged slightly smaller in first-year than in adult individuals. It may be noted that the two immature specimens taken in September have newly grown feathers of the throat and anterior breast that are conspicuously marked; the male (TNHC 1269) falls in class 2 and the female (TNHC 1263) in class 1. Also a juvenal-plumaged specimen from Tamaulipas (USNM 158851) has pale dusky brown markings on the throat (class 1). Thus all known immature specimens in our series show remnants of a throat patch.

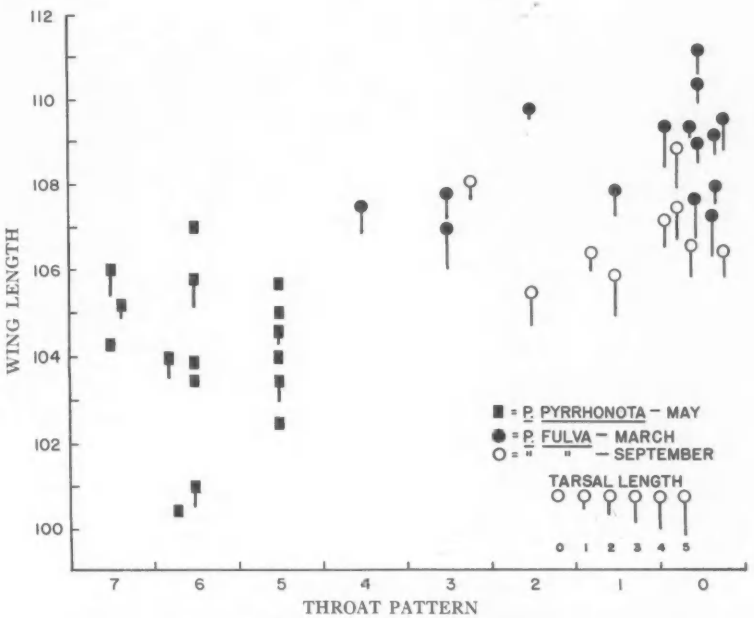

Fig. 8. Scatter diagram of males of *Petrochelidon* from central Texas showing wing and tarsal length and throat pattern. Six categories of tarsal length are used; length of line is proportional to actual tarsal length. See text for further explanation.

Wing length might be expected to average slightly smaller in first-year than in adult individuals even though the postjuvenal molt is complete. Presumably the March and June sample of *P. f. pallida* includes both adult and first-year birds and the September sample includes some birds which are undergoing their first postnuptial molt and are thus in the process of losing their first-year status. Since wing length in the latter sample represents length of old primaries acquired in the previous annual molt (see page 353), any differences in length between adult and first-year wings would be as apparent as in the March and June sample. The important point is the absence of correlation between throat pattern and length of two skeletal parts which are subject to continuous growth until adult size is reached, namely bill and tarsal length. Measurements of bill and tarsal length of two specimens undergoing postjuvenal molt indicate that these structures reach adult size before the molt is completed. In nestling Cliff Swallows studied by Stoner (1945:211) in New York, the tarsus reached adult size 12 to 13 days after hatching.

Considering the evidence presented, we conclude that variation in throat pattern in populations of the two species does not result from present-day hybridization. The possibility remains that genes determining throat pattern were exchanged through hybridization at some time in the past, perhaps when *P. pyrrhonota* and *P. fulva* first came into secondary contact and before reproductive isolation was complete. But as an alternative explanation we suggest that the remnants of the throat patch present in *P. fulva* may represent vestiges of a character possessed by the common ancestor of the two species, which has been retained or further developed in *P. pyrrhonota* and largely lost

Table 3

Variation in Throat Pattern in Adult and First-year Birds

Form	Date	Sex	No.	Classes of Throat Pattern 0	1	2	3	4	5	6	7	Per cent with throat marks
P. p. tachina	May, June,	♂	17						6	8	3	100.0
(Texas)	1914	♀	9					1	3	3	2	100.0
P. f. pallida	March, June,	♂	15	10	1	1	2	1				33.3
(Texas)	1914	♀	9	6	3							33.3
P. f. pallida	September,	♂	10	5	2	1	2					50.0
(Texas)	1956	♀	11	7	1	1	1	1				36.4
P. f. pallida	April, May,	♀	4	4								00.0
(Mexico)	1902											
P. f. subsp.	----------	♂	4	4								00.0
(Antilles)		♀	6	4	2							33.3

in *P. fulva*. In any event, they are present, although very weakly indicated, in two of the 10 specimens of *P. fulva* from the Greater Antilles which we have at hand and are thus not unique to populations sympatric with *P. pyrrhonota* (table 3).

In color and pattern, although apparently not in size, *P. p. melanogaster* of the central plateau of México and Oaxaca more nearly resembles *P. f. pallida* than does *P. p. tachina*. In *P. p. melanogaster* the forehead is chestnut or cinnamon rufous and the throat patch is often indistinct and only slightly glossy. The chin, throat, and sides of the head are rich chestnut, however, as in other races of *P. pyrrhonota* (Ridgway, 1904: 51). Measurements of *P. p. melanogaster* given by Ridgway (*op. cit.*: 52) and van Rossem and Hachisuka (1938) indicate that it is about the same size as *P. p. tachina*.

In two male specimens of *P. pyrrhonota* in the Texas Natural History Collection from the Big Bend region of western Texas, the throat patch is very small (class 3), and in one (TNHC 1073 from Black Gap, Brewster County) the forehead is cinnamon brown. The throat patch is somewhat larger in three other breeding specimens from Presidio County, but the skins are prepared in such a fashion that the extent of the patch cannot be determined accurately. Both *P. p. tachina* and *P. p. melanogaster* have been reported breeding in Brewster County (Van Tyne and Sutton, 1937: 58–59; Thompson, 1953: 171; and Phillips and Thornton, 1949: 119), and Van Tyne and Sutton noted that individuals closely resembling *P. p. melanogaster* of western México are present in small numbers in breeding colonies of *P. p. tachina*. These authors concluded that four of their 31 breeding birds from Brewster County "are actually representatives of *melanogaster*," rejecting the hypothesis that they are variants of a population most of whose members are referable to *P. p. tachina* and raising the question of whether or not *melanogaster* and *tachina* are conspecific. Material at our disposal is inadequate to solve this problem, but it may be noted that the forehead of a specimen of undetermined sex collected on June 27, 1948, in Presidio County (TNHC 221) is intermediate in color between the two forms, thus suggesting intergradation.

VOCALIZATIONS

As adequate accounts of the vocalizations of the Cave Swallow are not available, the following brief descriptions, taken from tape recordings made at the Dunbar Cave colony, may be of some interest.

Typically the song consists of a series of squeaks blending into a complex melodic warble and ending in a series of double-toned notes in which a *gua* sound and a very low *nock* sound are given simultaneously. Often a sharp *eep* note terminates the song.

In some instances the elements of the song do not follow the usual sequence or are given separately. A complete song lasts 3 seconds. At Dunbar Cave on April 6 birds were singing from their nests, and on several occasions birds sang in flight as they circled above the cave entrance. Conflict between birds for nests was much in evidence, accompanied by high-pitched, nasal *che* notes. The song was occasionally given in late September by birds perched on their nests in Dunbar Cave.

The song of *P. fulva* clearly corresponds to the "defiance" song of *P. pyrrhonota* given in connection with territorial and aggressive displays and described by Emlen (1952:180) as "a series of high thin squeaks and low gutteral gratings alternating in an extended song . . . ." In Texas at least, the song of *P. pyrrhonota* is much shorter than that of *P. fulva* and lacks the melodic warbling phrase.

In flight while leaving or returning to the cave, Cave Swallows keep up chattering choruses of short calls, which seem to consist of a great variety of different notes. However, repeated listening to recordings of these choruses revealed that only three basic types of calls are given. By far the most frequent of these is a short, clear *weet* or *cheweet* given at medium pitch with either a rapidly ascending or, less commonly, descending inflection. The next most frequent call is a very loud, sharply accented, and high pitched *che* or *chu* note, usually given in series of two to four. This became the dominant call of individuals which were disturbed by our presence in the cave and which were circling rapidly in a compact flock preparatory to leaving the cave. The third call is somewhat similar to the second but is a lower pitched, clearer *choo* and has a descending inflection. This was rarely given and then only by disturbed birds.

The *weet* and *cheweet* calls of *P. fulva,* which apparently function in maintaining flock integration, are similar to calls given by *P. pyrrhonota.* Perhaps the high pitched *che* or *chu* call corresponds to those "conversational" notes of *P. pyrrhonota* described by Emlen (1952:180) as a low *kersh,* modified under excitement to a higher pitched *ash ash.* The third call of *P. fulva* noted previously is similar to the alarm call of *P. pyrrhonota* described by Emlen (*loc. cit.*) as a "clear plaintive *zeoo* with a descending inflection," but from our limited experience we are not prepared to state that it has a warning function in *P. fulva.*

Navigation in the caves.—Since Cave Swallows do not penetrate into caves beyond the twilight zone it is improbable that they have need of a special acoustic orientation system such as that possessed by *Steatornis,* a bird which roosts and flies in totally dark parts of caves (Griffin, 1955). To test this possibility, however, we captured a dozen individuals in Dunbar Cave and released them singly in totally dark chambers and large passageways of the cave well in beyond their nesting chamber. Some birds were released in the center of large chambers, while others were released a foot or two from the cave wall. Almost invariably the birds fluttered to the top of the cave and hovered against the ceiling, often circling slowly around the chamber or passageway. None gave audible vocalizations at any time. As the birds circled, their wings almost continuously brushed against the roof and walls of the cave, producing a clearly audible swishing sound. It was apparent that the swallows detect surfaces by brushing their wings against them as they move about with hovering flight. Possibly at close range they also detect air currents reflected from surfaces but this remains to be tested experimentally. If a bird happened on to a large crevice, ledge, or eroded depression it would perch and some individuals managed to cling to roughened areas on the wall, but some birds finally fluttered to the floor exhausted after several minutes of hovering flight. We noted that none undertook straight-line flight along the passageways or attempted to leave the immediate region of the cave in which they were released, behavior which might be expected if the birds were able to navigate by echolocation.

To test further the possibility that echolocation was being used, however, we tightly plugged the ears of five birds with balls of moist cotton and released them in total darkness after making certain that they had been given no opportunity to see the walls of the chamber in which they were released. The behavior of these birds did not differ in any way from that of birds which we had previously tested or from that of five controls released at the same time.

SUMMARY

In Texas the Cave Swallow (*Petrochelidon fulva*) nests colonially in the twilight zone of limestone caves along the southern edge of the Edwards Plateau from Val Verde County east to Kerr County; all caves known to be inhabited are described. Ecologic isolation limits contact between the Cave Swallow and its sympatric congener, the Cliff Swallow. It is suggested that in Texas and New Mexico nesting of the Cave Swallow is restricted to caves by competition with the Cliff Swallow.

The Cave Swallow is resident in Texas from early February to late September or, possibly, early October; laying begins in early April. Adults undergo postnuptial molt prior to fall migration.

The nest is an unroofed half-cup shell composed of pellets of mud and/or guano and lined with feathers and plant fibers. Nests are re-used year after year, becoming progressively larger as additional layers of pellets are added to the rims. Cave Swallows show a strong tendency to build their nests in isolated crevices and pockets or close up under overhanging ledges, in positions well screened in all directions from neighboring nests. Apparently this behavior achieves the same end as does the roof of the nest of the Cliff Swallow, namely that of increasing social stability by reducing territorial conflict.

Thirty-four per cent of specimens of Cave Swallows from Texas show remnants of a dark throat or breast patch, resembling in shape and position the posterior part of the metallic throat and breast patch present in the Cliff Swallow. The hypothesis that this condition results from present-day hybridization with the Cliff Swallow is examined and rejected. Instead it is suggested that it represents a vestige of a character possessed by the common ancestor of the two species.

The vocalizations of the Cave Swallow are compared with those of the Cliff Swallow. The songs of the two species are rather distinctive, the other calls less so.

The possibility that Cave Swallows have a special acoustic orientation system for navigating in caves was tested experimentally, with negative results.

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DIURNAL CYCLES IN LIVER WEIGHTS IN BIRDS

By HARVEY I. FISHER and LAWRENCE M. BARTLETT

While gathering data for a study of changes in organ weights during various phases of the reproductive cycle of Red-winged Blackbirds (*Agelaius phoeniceus*), we were first struck by a difference in the color of the liver of birds collected in the morning compared with others collected in the evening. We thought differences in constituents might be causing the color variations, and this prompted us to compare liver weights. The great overnight drop in liver weight led to a preliminary study to determine the factors involved in the daily changes noted.

Further, we were unable to find in the literature any reference to diurnal cycles of weight or constituents of the liver in normal, wild animals except in Odum and Perkinson (1951:217) who stated that birds were collected "in the late afternoon, so as to minimize daily variations in lipid content." Since nothing further about "daily variations" was mentioned in their paper we assume they were exercising normal care in obtaining a homogeneous sample based on their knowledge of the literature describing diurnal cycles of fat, glycogen, and protein in laboratory animals.

Another factor emphasizing the importance of information on a possible diurnal cycle in liver weight is that in virtually none of the multitude of papers on the liver is there any mention of the time of day when the animals were killed; the papers by Odum and Perkinson (1951) and Oakeson (1953, 1956) are exceptions. If there is a diurnal cycle in liver weight and in fat, protein, or carbohydrate constitutents of the liver, data presented without precise information on time of collection of the specimens is of no value for comparative purposes.

MATERIALS AND METHODS

Collections.—While netting the Red-wings we also took a number of Starlings (*Sturnus vulgaris*); data from these are included. The specimens used in this study were either shot or captured at their roosts in a Japanese "Mist Net" between February 16 and March 27, 1956, in the vicinity of Carbondale, Jackson County, Illinois. The major part of the collection was made between February 27 and March 21. Time of kill is given in the tables. No significant differences were found between the mean body or liver weights of birds shot and birds netted. Furthermore there appeared to be no difference in these average weights between 12 female Red-wings held in cages outdoors (30°F.) and 14 female Red-wings held in cages indoors (70°F.). In addition there was no difference between birds netted and killed in the morning as compared with those netted in the evening and held over, without food, to be killed the following morning. In Red-wings there was no significant difference in the data between adult and first-year males. Therefore, the data from the various collecting and handling procedures have been combined for the statistical treatment of the differences between sexes and times of day.

One group of 27 female Red-wings (table 2), held for 12 or more hours, was provided with scratch food and water, but when they were killed we found no significant evidence that they had fed. The Starlings (table 3) were held without food and water.

A total of 45 male and 72 female Red-wings and 20 male and 11 female Starlings were used in this study.

Weights.—Body weights were obtained from a triple-beam balance accurate to 0.1 gram; liver weights were measured on a Roller-Smith torsion balance, to the nearest milligram. The livers were removed as soon as possible after death. In most instances this was within one-half hour, but all specimens were worked up within one and one-half

hours. As each liver was removed, it was freed of any extraneous tissue and blotted on paper towels before being weighed. Each liver was then divided. One part was weighed, placed in ethanol-ether (3:1) and stored in the refrigerator for later quantitative analysis of the lipids. The other part was placed in a dry shell vial, corked, and quick-frozen for glycogen analysis.

Chemical methods.—During the analysis of fats a short circuit in the refrigerator in which the samples were stored ignited the ether, causing an explosion and fire which destroyed 37 of the 80 samples of fat. The pieces of liver for glycogen analysis were stored in the freezing unit of the same refrigerator, but 52 of the original 78 samples appeared to be unharmed. Nevertheless, a few "odd" results in our data may be attributed to this accident. Although we cannot attach too much significance to the individual results, we feel that the trends shown justify the inclusion of the data on fat and glycogen analysis, pending a more complete study.

The analysis of fats was carried out according to Bloor's (1928) titrimetric method. We used a factor of 3.7 in the calculations to arrive at our estimate of total fat.

Since the separation and purification of the glycogen was a combination of several procedures (Consolazio, Johnson, and Marek, 1951; Snell and Snell, 1953; and Wagtendonk, Simonsen, and Hackett, 1946) we shall describe the steps briefly. The liver sample was placed in a 15-ml. centrifuge tube with sufficient 35 per cent KOH to cover it. This was heated in a boiling water bath for 30 minutes, with occasional shaking, until the sample was completely digested. After cooling, 95 per cent ethanol was added, the solution mixed vigorously with a platinum wire, and then immersed in hot water to bring the alcohol just to its boiling point. It was then centrifuged while warm, the supernatant decanted, and the residue dissolved in 5 ml. of warm water. One drop of Lugol's solution was added, and the color read at a wavelength of 470 in a colorimeter against a reagent blank. The amount of glycogen was determined in the usual manner from a calibration curve.

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We wish to express our appreciation to the Graduate School of Southern Illinois University for financial aid and to Mr. Harold Ward, a student chemist, for his chemical analyses of the livers.

RESULTS

Changes in weight.—Figure 1 and tables 1 to 3 summarize the body and liver weights and the ratio of liver to body weight. In comparing any two means, a "t" test was used to determine the probabilities discussed in the text.

Although the body weight of male Red-wings decreases slightly during the night, both actual and relative liver weights decrease more rapidly. Data in table 1 show that the liver weight in male Red-wings decreases by one-third during a 12-hour night period. When the ratio of liver to body weight is considered, the overnight decrease is nearly as great (30 per cent).

Data in tables 1 and 2 show that both the relative and actual overnight decreases in body weight are greater in females than in males—10.7 versus 4.5 per cent and 5.2 versus 3.2 grams, respectively. Males show a greater loss in liver weight overnight than do females (33 versus 22 per cent). When calculated as per cent of body weight, liver weight in the males drops 30 per cent; in females this relative loss in weight is about 12 per cent. Part of this apparently lesser loss in females may be attributed to their greater loss in body weight.

Since we have no data for males killed after being held in captivity for more than 12 hours, we have no basis for distinguishing sexual differences in the changes in body

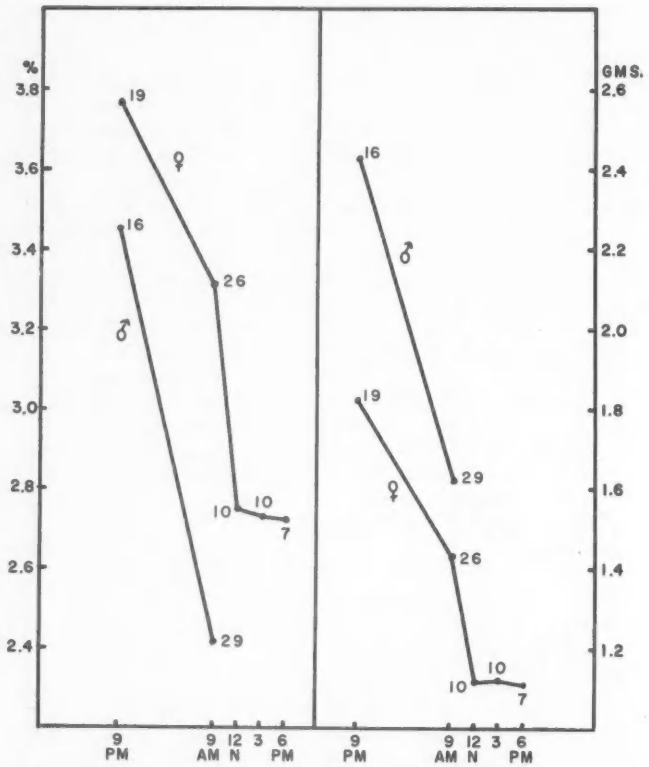

Fig. 1. Liver weights of Red-winged Blackbirds. Left, weights expressed as per cent of body weight. Right, weight in grams.

or liver weight beyond the overnight period. Although females (table 2) showed no significant loss in body weight after 9 a.m., even though they had not fed, the actual liver weight between 9 a.m. and noon decreased by 19 per cent and the relative liver weight went down 17 per cent. After noon there was no further significant change in either actual or relative liver weights.

Although we had only a small sample of Starlings (table 3), it would appear that the body weight of male Starlings decreases more (15 per cent) in the overnight period than it does in females (9 per cent). This is the reverse of the situation we found in the Red-wings (tables 1 and 2). The data on male Starlings, as on female Red-wings, after a 12-hour period in captivity do not indicate any loss in body weight during that time.

There was nearly a 40 per cent decrease in liver weight in male Starlings between the time they were captured in the evening and late the following morning; females showed only a 25 per cent decrease during the same period. The ratio of liver weight to body weight decreased 29 per cent for males and 18 per cent for females in this period. In these respects, the data from the two species are comparable.

Table 1

Body and Liver Weights of Male Red-winged Blackbirds

	Number specimens	Mean	Range	Standard deviation	Coefficient of variation
		Body weight in grams			
5–8 p.m.	16	70.4±1.28	63.0–77.4	4.96	7.0
6–10 a.m.	29	67.2±0.76	58.6–78.9	4.00	6.0
		Liver weight in grams			
5–8 p.m.	16	2.424±0.110	2.010–3.110	0.348	14.4
6–10 a.m.	29	1.621±0.035	1.354–1.962	0.183	11.3
		Liver weight as per cent of body weight			
5–8 p.m.	16	3.45±0.14	2.63–4.19	0.448	13.0
6–10 a.m.	29	2.42±0.05	1.97–2.83	0.262	10.8

Table 2

Body and Liver Weights of Female Red-winged Blackbirds

	Number specimens	Mean	Range	Standard deviation	Coefficient of variation
		Body weight in grams			
9 p.m.	19	48.5±0.95	41.8–55.5	4.02	8.3
9 a.m.	26	43.3±0.78	36.8–52.0	3.91	9.0
12 noon	10	42.1±1.05	38.2–46.1	3.16	7.5
3 p.m.	10	42.6±0.58	40.0–44.6	1.73	4.1
6 p.m.	7	41.6±1.16	38.5–47.2	2.84	6.8
		Liver weight in grams			
9 p.m.	19	1.823±0.052	1.450–2.390	0.222	12.2
9 a.m.	26	1.424±0.033	1.120–1.782	0.164	11.5
12 noon	10	1.155±0.039	0.981–1.436	0.118	10.2
3 p.m.	10	1.162±0.064	0.822–1.461	0.191	16.4
6 p.m.	7	1.130±0.068	0.925–1.319	0.167	14.8
		Liver weight as per cent of body weight			
9 p.m.	19	3.77±0.09	3.00–4.34	0.394	10.5
9 a.m.	26	3.31±0.09	2.47–3.96	0.449	13.6
12 noon	10	2.75±0.07	2.51–3.11	0.214	7.8
3 p.m.	10	2.73±0.14	2.06–3.30	0.412	15.1
6 p.m.	7	2.72±0.14	2.32–3.26	0.333	12.2

Changes in fat and glycogen.—Data in table 4 show that the fat content dropped overnight in Red-wings and Starlings. It increased again during the following afternoon in the male Starlings and female Red-wings. It may be recalled that the Starlings were held without food or water whereas the Red-wings had access to both but apparently did not eat.

Data in table 5 indicate that the glycogen content of the liver also dropped overnight. However, the drop was undoubtedly not as great as indicated by the averages since the three specimens possessing extreme glycogen supplies (11.5, 20.2, and 14.6 mg./gm., maxima) were all killed in the evening. These "extreme" results tend to raise the average value of the evening group of birds and thus increase the apparent overnight drop. Whereas the fat content appeared to make a recovery during the afternoon, the data suggest that there was little or no glycogen recovery during this period.

Table 3

Body and Liver Weights of Starlings Killed at Different Times of Day

	Males				Females			
	No. spec.	Mean	Range	Standard deviation	No. spec.	Mean	Range	Standard deviation
			Body weight in grams					
First p.m.	5	88.3±2.18	84.3–94.0	4.36	7	78.8±0.83	76.1–80.7	2.03
Morning	8	75.2±0.74	62.8–82.3	1.95	3	71.6±2.33	68.4–75.0	3.30
Second p.m.*	7	73.2±2.18	67.5–83.6	5.34				
			Liver weight in grams					
First p.m.	5	3.55±0.310	2.64–4.21	0.620	7	3.29±0.149	2.95–3.98	0.366
Morning	8	2.17±0.090	1.81–2.54	0.239	3	2.46±0.198	2.13–2.64	0.281
Second p.m.*	7	2.09±0.133	1.83–2.73	0.326				
			Liver weight as per cent of body weight					
First p.m.	5	4.04±0.390	3.07–4.94	0.779	7	4.18±0.165	3.67–4.93	0.402
Morning	8	2.89±0.114	2.58–3.44	0.301	3	3.43±0.221	3.11–3.69	0.313
Second p.m.*	7	2.86±0.171	2.33–3.63	0.419				

* Held in captivity for 24 hours.

DISCUSSION

Decreases in weight, fat, water, glycogen and protein have been shown by Higgins, Berkson, and Flock (1932, 1933) in rats deprived of food and water for 24 hours, but nowhere have we been able to find reference to a normal diurnal change in liver weight of any animal. This seems strange in view of the diurnal fluctuations in liver fat and glycogen which have been demonstrated in various laboratory animals. One would expect some change in gross weight of the organ as a result of changes in fat and glycogen content. However, one would certainly not expect, from anything in the available literature, that an overnight drop of about 30 per cent would occur. The magnitude of the fluctuation, then, was one of the most striking aspects of our study.

In our data the apparently greater drop in liver weight shown by the Starlings is probably not real. Most of the morning Starlings were sacrified later in the morning (about 11 a.m.) than the Red-wings. If we graph the drop in liver weight of the Red-wings we find that, by 11 a.m., the decrease was comparable to that shown by the Starlings. Therefore, it seems justifiable to assume that the degree of loss in liver weight may be comparable in the two species.

Weekly differences.—Seasonal differences in organ weights have been demonstrated for many species of birds. Since our collections were made at a time when at least some individuals of the species were in migration, and since Odum and Perkinson (1951) have demonstrated that fat deposition may occur over a very short period of time prior to the spring migration in the White-throated Sparrow (*Zonotrichia albicollis*) we were led to compare, at weekly intervals, the liver weights of female Red-wings during the three-week period over which most of our collections were made (table 6). Although there was little if any statistically significant weekly difference in mean liver weight of birds collected at the end of the day, there seemed to be a highly significant difference in birds collected in the morning. The morning values of 1.23 and 1.31 (first and second weeks) are not significantly different, but 1.31 and 1.56 (third week) are different (1 in 1000) and 1.23 and 1.56 are different (1 in 10,000). Thus, there was exhibited a trend of lesser overnight decrease in liver weight during the period of the study. Despite this trend, the differences between evening and morning weights remained significant (table 6). It may also be worth noting that the coefficient of variation is generally greater for evening than for morning liver weights. These data suggest the possibility

that the female Red-wings were using stored materials in the liver at a greater rate during the nights of the week of February 27-March 4 than was the case between March 12 and 18.

Fat depletion overnight.—Our data are not sufficient to say with certainty whether the loss of fat from the liver could account fully for the loss in weight of the liver between 9 p.m. and 9 a.m. However, the four female Red-wings (table 4) sacrified at 9 p.m. and the five sacrified at 9 a.m. suggest this possibility. The average total amount of fat "lost" was 243 mg. while the average liver weight "lost" was only 190 mg. This suggests, ignoring possible quantitative errors in the chemical procedures, that some other constituent may be increasing while the fat is being depleted, but not at a rate which prevents a pronounced drop in liver weight. In spite of the fact that these nine birds did not show as great a drop in liver weight (1.77 to 1.58 gms.) as would be indicated by our other data, it would appear that changes in the fat content may account for the major, if not entire, observed drop in liver weight.

Table 4

Fat Content of Liver

Time	Sex	Number specimens	Av. mg./gm. fresh weight	Range
		Red-wings		
p.m.	♀	4	228	155–379
a.m.	♀	5	99	31–174
3 p.m.	♀	2	174	144–204
6 p.m.	♀	2	258	169–347
		Starlings		
9–12 p.m.	♂	3	187	110–234
	♀	6	262	65–439
Noon	♂	6	108	68–168
9–12 p.m.	♂	5	212	12–367

Comparison with other species.—Riddle (1928) working with the Ring Dove (*Streptopelia risoria*) found the liver weight greater in the female than in the male at all four seasons of the year, but it should be noted that in this species the female is the heavier sex. Oakeson (1953, 1956) found in the non-migratory race of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) that the liver weight of the female was greater than that of the male only in the spring of the year. Stegeman (1954) studied the body weight and weight of various internal organs in a group of 455 Starlings captured on a single night, chloroformed, kept in a cold room overnight, and weighed in groups of 50 on the following day. Stegeman gave the liver weights as male (4.110±0.04) and female (3.823±0.04); comparable data of ours are 3.55±0.31 and 3.29±0.15, respectively. In terms of body weight, he gave the liver as 5.0 per cent in both sexes, and we calculated it as about 4.0 per cent. The higher weights of livers of Stegeman's Starlings probably reflected the coagulated blood contained in them as a result of his method. The greater variability in the liver weights of our birds resulted perhaps from some differential retention of blood in fresh specimens and quite probably from the small size of our sample.

Whereas our data tend to be in agreement with Stegeman's statement that the liver weight of the male Starling is greater than that of the female, this is true only for birds collected in the evening. In others collected in the morning, our data indicate that the liver weight of the male is insignificantly less than that of the female.

When liver weight is considered as per cent of body weight, the female is "heavier" in the morning in both Starlings and Red-wings, whereas there appears to be no differ-

ence between sexes in the evening. However, during the night the male Red-wing loses only 5 per cent of its body weight and the female 10 per cent. In Starlings the male's body weight drops 15 per cent and the female's less than 9 per cent.

It may well be that the greater decrease in the female Red-wing's body weight accounts for all of the relatively larger liver in that sex. However, there is the possibility that the physiological events occurring in the liver during the period of sleep are different, at least in magnitude, between the sexes. Clavert (1944) has shown that administration of estrogen increases liver fat and protein as well as the number and size of the liver cells. The possible sex difference indicated in our work might, therefore, be attributed to the influence of estrogen on fat and protein content. Our data are not yet sufficient to say with certainty that there is any difference in the fat content of the liver between sexes at different times of the day.

Odum and Perkinson (1951) suggested that total lipids in the female White-throated Sparrows may be greater than in the male, especially in the premigratory period, when total lipids are considered as per cent of body weight. In their midwinter period (January-February) which is most comparable perhaps to the period of ours of late February to mid-March, they reported that 10.4 per cent of the fresh weight of the liver is lipid material in birds collected in "late afternoon." Because no definite time of collection was stated, it is impossible to know whether their data are comparable to our 3 p.m. kill (table 4) or to our 6 p.m. kill, but in any case our observed values seem to be considerably higher. Their data cannot be compared to our "p.m." data secured from birds killed, for the most part, between 9 p.m. and midnight.

The data of Musacchia (1953) cannot be used for comparison, partly because of seasonal differences, but primarily because there is no indication of the time of kill of the birds. There is, of course, no evidence to indicate any diurnal cycle or sexual difference in the livers of the species he studied, but perhaps only because this aspect has not been investigated.

In any event, it appears that the avian species thus far studied, regardless of the time of day, have a higher lipid content in the liver than do the familiar laboratory mammals (3 to 5 per cent).

Glycogen content of the liver in Starlings and Red-wings dropped between 9 p.m. and 9 a.m. and then maintained its level for at least 9 to 12 hours under starvation conditions. Fat content has just been shown to increase after a low at 9 a.m. Thus our data

Table 5

Glycogen Content of Liver

Time	Sex	Number specimens	Av. mg. per gm.*		Range
		Red-wings			
9 p.m.	♀	4	4.98		1.47–11.50
9 a.m.	♀	10	2.34		0.94– 6.71
Noon	♀	3	2.65		1.72– 4.13
3 p.m.	♀	3	1.17		0.75– 1.92
6 p.m.	♀	6	2.18		0.77– 4.86
		Starlings			
10 p.m.	♂	2	12.85	9.64	5.50–20.20
	♀	3	7.51		3.85–14.63
Noon	♂	6	2.27	2.28	1.35– 5.32
	♀	2	2.29		2.02– 2.56
10 p.m.	♂	6	2.68		1.63– 6.36

* Mg./gm. fresh liver weight in Red-wings and mg./gm. frozen liver weight in Starlings.

possess limited agreement with those of Petrén (1939) who found a maximal glycogen content in guinea pig livers between 11 a.m. and 3 p.m. and a minimal level between 5 and 9 a.m. and with those of Marble, Grafflin, and Smith (1940) who found no differences in glycogen, fat or water content in guinea pig livers between 9 a.m. and 3 p.m.

MacLachlan *et al.* (1942), Ota (1940) and Chevillard, Hamon, and Mayer (1937) reported accumulation of fat during fasting in several species of rodents. Ohlsson and Blix (1934, *in* Bloor, 1943) reported that in rats a high-fat phase coincides with a low-glycogen phase and vice versa. Our data for evening birds do not support this thesis; data on birds held under fasting conditions do corroborate the reverse relationship.

These comparisons with mammals may be specious. Liver metabolism is highly variable and in some studies (Kilborn, 1939) livers of birds have been shown to differ from mammals in that the type of fat stored in the bird's liver differs according to the type of fat in the diet.

Table 6

Comparison of Morning and Evening Liver Weights of Female Red-winged Blackbirds by Weeks

	Feb. 27–Mar. 4		March 5–11		March 12–18	
	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.
Sample size	9	17	5	5	6	7
Liver weight						
Mean	1.87±0.09	1.23±0.04	1.66±0.08	1.31±0.03	1.83±0.10	1.56±0.05
Range	1.46 – 2.39	1.00 – 1.52	1.45 – 1.86	1.20 – 1.36	1.68 – 2.10	1.43 – 1.78
Standard deviation	0.27	0.15	0.16	0.06	0.21	0.12
Coefficient variation	14	12	10	5	12	8

It does appear that fat moves into the liver from various fat depots during fasting, and we may presume that the 12-hour overnight period is one of fasting. Since glycogen is high in the evening, the transport of fat to the liver for conversion to glycogen and energy is not rapid during the first 12 hours of fasting and both the fat and the glycogen show overnight decreases. As fasting, or insufficient intake of food compared to energy requirements, goes on during the next day, glycogen reaches minimal levels and fat is moved to the liver more rapidly than it is converted to glycogen. Hence, fat levels in the liver go up in the afternoon—perhaps partly from fat depots and partly from food ingested during the day. If the high metabolic rate of birds permits rapid acquisition of glycogen from daily food and rapid conversion of fat to glycogen, it is possible that glycogen levels in birds may be lower than in mammals.

SUMMARY

A pronounced diurnal fluctuation in liver weight has been demonstrated in Red-winged Blackbirds and Starlings.

Based on small samples it appears that both fat and glycogen stores in the liver decrease overnight and that the decrease in fat content is primarily responsible for the observed loss in liver weight. The fat and glycogen content of the liver is highest sometime in the early evening, and, for Red-wings and Starlings, seems to exceed any previously published values, probably because previously most work has been done on birds collected in the mornings when these constituents are near their minimum in the diurnal cycle.

Comparison of evening and morning liver weights of Red-wings and Starlings indicates that the male's liver weight drops more rapidly than that of the female.

During the three-week period from February 27 to March 18, the morning liver weight of female Red-wings increased, apparently as the result of a smaller overnight drop in weight. This suggests the possibility that, as spring comes on, a smaller amount

of stored food from the liver is necessary to supply the metabolic needs of the roosting bird.

Comparison with data on liver weights obtained by other workers shows the need for consistency in methods of gathering the data in terms of time of day and handling procedures if interspecific comparisons are to be valid.

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AN ANALYSIS OF AVIFAUNAS IN THE TETON MOUNTAINS AND JACKSON HOLE, WYOMING

By GEORGE WILLIAM SALT

Faunal analyses may be made for several purposes: to reveal ecologic characteristics of a community either of present times or, as is done by paleontologists, of past ages (Miller, 1937); to demonstrate pathways of energy exchange within an ecosystem (Turcek, 1952); or to evaluate ecological or evolutionary relationships between faunas (Miller, 1955; Snyder, 1950; Corti, 1952). The present analysis is an effort to secure results useful for all three. The primary object was to collect data on the bird life of an area in the Rocky Mountains for comparison with that of the Sierra Nevada. Results of the comparison will appear in a latter report on Sierran avifaunas. Herein are reported findings on community characteristics and trophic or feeding relationships as determined from analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming.

The work was done during the summers of 1952 and 1954 at the Jackson Hole Biological Station of the University of Wyoming, where facilities were kindly provided. Financial support was generously given by the New York Zoological Society for which I am grateful. I also wish to express my thanks for assistance to Mr. James Simon, former director, Dr. L. Floyd Clarke, present director of the station, and my colleagues and friends at the station. The weights used were taken from specimens in the Museum of Vertebrate Zoology at Berkeley; to Dr. A. H. Miller and Dr. F. A. Pitelka I express my gratitude for permission to use this material.

DESCRIPTION OF THE AREA

The Teton Mountains form the west wall of the valley of Jackson Hole in northwestern Wyoming. They rise abruptly from the valley floor (6900 feet) to peaks of 10,000 to 13,766 feet. The canyons, running at right angles to the axis of the range, are deep glaciated troughs draining eastward into a row of moraine-enclosed lakes along the base of the Tetons. The lower parts of the mountains and the canyons are forested up to about 10,000 feet, but avalanches, cliffs and talus slides make the distribution of vegetation varied and irregular. Alpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga taxifolia*) dominate at lower elevations; white-bark pine (*Pinus albicaulis*) dominates at higher elevations.

Jackson Hole is a narrow valley extending about forty-eight miles north and south; its greatest width is about twelve miles. The northern end is filled with the dammed waters of Jackson Lake from which the Snake River runs southwestward the length of the valley. The northern and eastern flanks of the valley are formed by the Yellowstone and Mount Leidy highlands while the Gros Ventre and Hoback mountains enclose the southern end. There are three towns: Moran at the northern end where the Biological Station is located, Jackson at the southern end, and Moose halfway between them. The predominant vegetation of the valley floor, sagebrush (*Artemisia tridentata*), is interrupted by groves of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*) forests, and, where the beavers have dammed the streams, willow (*Salix*) swamps. An association characterized by southern poplar (*Populus deltoides*) and blue spruce (*Picea pungens*) exists along the banks of the Snake River. Hills within the valley and around its margin are forested. The floristics of most of the vegetation types in the area have been studied in detail by Reed (1952). A more thorough description of the area may be found in papers by Fryxell (1938) and James (1936), and the geology and glacial history of the valley is dealt with in a paper by Fryxell (1930). Nearly all the area is now included in Grand Teton National Park.

During early summer the climate alternates between sunny days and thunderstorms that last several days. Freezing nights are not uncommon in late June. As the summer progresses, rainstorms sometimes become less frequent and freezing nights are rare or lacking. Maximum daytime temperatures are usually between 70 and 80 degrees F.

METHODS

In this study censuses were made by the strip-transect method. Birds were counted in four communities in Indian Paintbrush Canyon in the Tetons and in three vegetation types in the valley near the Biological Station. The strips were between one-half and one mile long, depending on how large a pure stand of the vegetation type could be found. In all instances the strips were sixty yards wide. Distances of thirty yards on either side of the route were paced off at intervals along the strip. I walked along the route at a rate of about one mile per hour recording each bird seen or heard within the strip. Notes on activity were made on birds seen. Counts were made during the morning hours, usually between 7:00 and 10:00 a.m.

There were several reasons for using this method in preference to plotting territories of singing males in a measured area: (1) The Sierran censuses with which these data were to be comparable were made on strip transects; (2) the irregular vegetation and rugged terrain make traversing a quadrat, assuming one large enough could be laid out, an exercise in mountaineering; and (3) the breeding seasons of the birds are not synchronized and some such as the Clark Nutcracker are finished before others have begun.

In the Rockies of Colorado twenty-one miles west of Boulder, Snyder (1950) censused in lodgepole pine and spruce-fir forests. Mapping territories in quadrats of 14.2 to 22.2 acres, he was able to get specific density figures for about half the species present. Although there are undoubtedly differences in climate and soil between that area and the Tetons, a comparison of the two regions is presented in table 1 in terms of birds per 100 acres.

Table 1

A Comparison of Densities of Birds in Two Areas of Coniferous Forest

Habitat	Species	Area	
		Colorado	Wyoming
Lodgepole pine forest	Mountain Chickadee	9/100 ac.	6.7/100 ac.
	Siskin	23	1.7
	Junco	5	10.0
Spruce-fir forest	Hairy Woodpecker	7	2.8
	Mountain Chickadee	12	7.0
	Hermit Thrush	8	3.5
	Ruby-crowned Kinglet	28	8.4
	Audubon Warbler	6	7.7
	Pine Grosbeak	4	3.5

Although there are obvious discrepancies, the two sets of figures agree sufficiently to suggest that the strip-transect counts can be converted into densities with reasonable confidence. It is uncertain whether the strip method underestimates densities or whether the Wyoming figures are generally lower because of habitat differences.

TREATMENT OF DATA

The findings for each vegetation type are given in tables 2 to 7. Profiles (fig. 1) of three of the vegetation types are presented to show the foraging niches of the inhabiting birds. (I am indebted to Dr. T. I. Storer for suggesting this technique.) Nearly all the species considered in this report are shown.

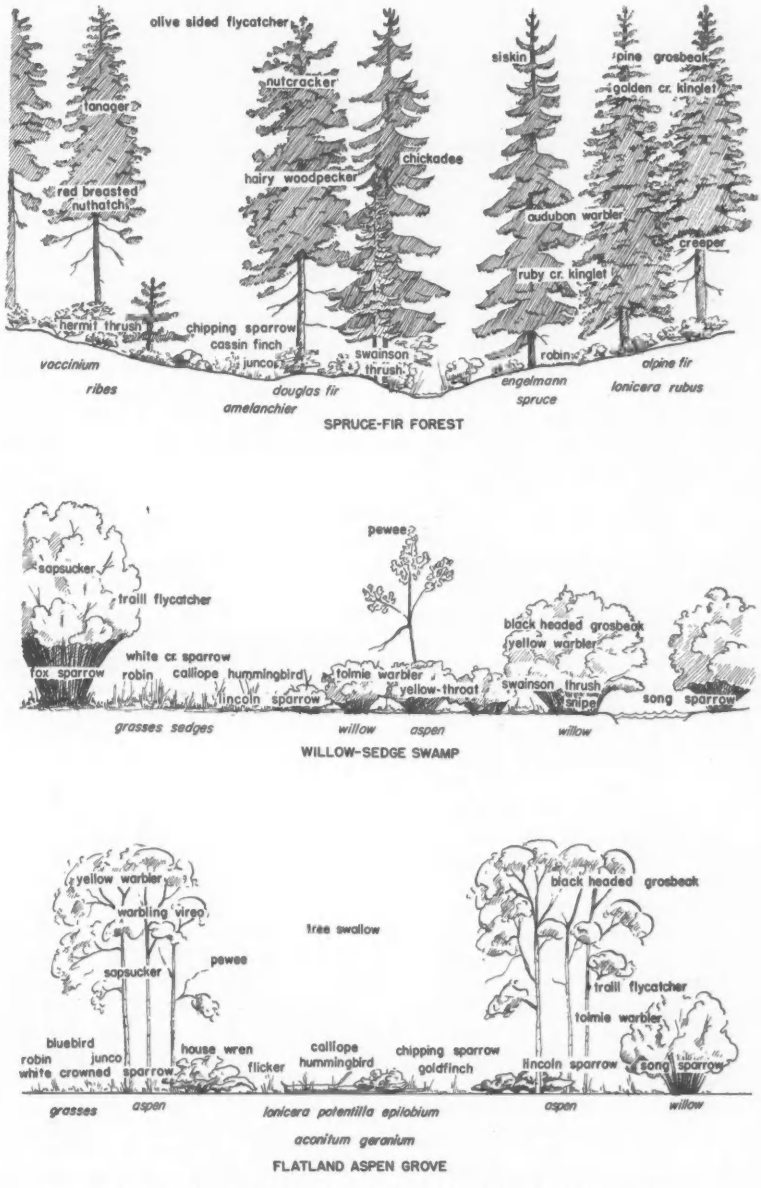

Fig. 1. Vegetation profiles showing foraging niches of the inhabiting species.

Census figures in the accompanying tables are given as mean numbers of individuals counted per trip. These are then converted to the standard value of birds per 100 acres. The species are listed in their feeding categories according to foraging level and food type as described in an earlier paper (Salt, 1953). One modification has been made; air feeders have been subdivided into soaring (A–S) and perching (A–P) categories. Other categories are: Foliage-nectar (F–N), Foliage-insect (F–I), Foliage-seed (F–S), Timber-searching (T–S), Timber-drilling (T–D), Ground-predator, (G–P), Ground-insect (G–I), and Ground-seed (G–S).

Turcek has inquired (letter) why I classified all species into either insect or seed eaters rather than using an additional category of mixed feeders as he has done. There is no doubt that these birds form an important group in any avifauna as he has shown. However, I wished to determine values for herbivore (primary consumer) and carnivore (secondary and tertiary consumer) biomasses (total weight of living material) and to do this each species must be placed in one or the other category. The mixed feeders were placed, then, according to which type of food formed the largest part of the diet.

At first thought it might be argued that food habits for the species should be determined for the area investigated. There can be no doubt that this would result in increased accuracy in classification of some species, especially if the further refinement were made of partitioning a biomass into categories according to the percentage of food of each type in the diet. However, a gram of insect material cannot be assumed to be necessarily equivalent to a gram of plant material or for that matter equivalent to dissimilar insect food. In view of this, there seems to be no great increase in accuracy possible without a simultaneous determination of caloric content of the food. I regard the latter procedure as highly desirable, but a program of food analysis of this magnitude could not be carried out at Jackson Hole.

If an avifauna is to be measured, some sort of unit must be used. Furthermore, the results must be expressed as multiples of that unit. The simplest characteristic to measure is the number of species making up the avifauna. If the generalization is accepted that each species occupies a unique niche, then the number of species gives an indication of ecologic diversity in the habitat. The total species composition of the seven avifaunas studied is shown in table 9.

Avifaunal composition is frequently expressed as numbers of individuals. I must admit that the value of this expression is not clear to me. It seems to imply that in some way three horned owls and one hummingbird are equal to four sparrows. What would seem to be a more meaningful measure is that given when these individual numbers are multiplied by the weight for each species. When this is done the results appear as one kind of biomass, standing crop biomass, that is, the biomass present at the time of census. These standing crop biomass figures indicate the total weight of the birds present on a unit area. Considering the matter from the point of view of community metabolism, they represent the total stored energy present as birds, or putting it another way, the amount of food available for things that eat birds. In the tables the total standing crop biomass is given for each feeding category.

A figure related to food consumption may be derived from the standing crop biomass by making use of a generalization from the field of bioenergetics. The conversion is made for each species by multiplying numbers of individuals times the mean weight of the species to the 0.7 exponent and then summing all the values for an avifauna or some part thereof. The resulting figures are referred to here as "consuming biomass." These can be taken as indicative of rate of food consumption or energy intake by the avifauna.

The reasoning in support of this method is as follows. Oxygen consumption per gram and hence calories consumed from one species or individual to another is known to be

proportional to a mathematical derivative of body weight (Brody, 1945:352–374)—an exponential function. The precise value of this exponent has been a matter of some dispute; suggested values range from 0.62 to 0.73, but acting on advice from Dr. William R. Dawson, who is studying this subject, I have used 0.7. Even if the theoretically correct value proves to be somewhat different, using it would not improve significantly the accuracy of the figures given here.

When weights to the 0.7 power are used the lower metabolism per gram of large birds relative to small ones is cancelled out and all weights thus modified become equal in terms of caloric intake per gram under standard conditions at a given temperature.

It would be erroneous to argue that these values for consuming biomass could be converted to actual food consumption values in the wild if we only knew the correction factor to use, for two variables still remain uncorrected, environmental temperature and species differences in temperament. The major variable, temperature, actually introduces no great error for comparisons when the avifaunas considered have similar proportions of large and small species and are all in neighboring communities subject to the same macroclimatic regime. Under these circumstances the food consumption by all the avifaunas would experience parallel increases and decreases in response to temperature fluctuations and hence would remain comparable. One might argue that different species show different abilities to consume food at extreme temperatures, particularly cold. Dawson (1954), Salt (1952), Seibert (1949), and Kendeigh (1949) have shown, however, that species residing in a place having extreme weather are adapted to these conditions. The significant variable is, once again, size. If comparisons were to be made between avifaunas from significantly different climates, correction would undoubtedly be needed. That there are differences in temperament and activity rate between species is well known to all ornithologists. A phlegmatic vireo and an active warbler of the same weight certainly consume different amounts of food. Here, though, it seems probable the differences are small enough to be ignored for what are first approximations. On this basis, then, the "consuming biomass" figures are regarded as indices of food intake. They give no indication of absolute amounts of food required, but are useful for comparison. Two avifaunas may be regarded as consuming food at rates proportional to their respective consuming biomasses.

The weights used in the calculations are the means of samples in the Museum of Vertebrate Zoology collected nearest Jackson Hole. The birds are weighed when collected and the weight is recorded on the tag. It was not thought necessary to correct for sex and age distribution as suggested by Elton and Miller (1954). At the seasons when the censuses are made there are few birds present as immatures which are not recognizable as such. In addition, young birds rapidly reach adult weight after fledging. While there are differences between sexes, these were accounted for by averaging weights for both sexes and assuming an equal sex ratio.

For comparison with the results of the Wyoming study, biomass values have been calculated for avifaunas of three community successional series of the eastern United States: oak-hickory of the Georgia Piedmont (Johnston and Odum, 1956), beach-maple-hemlock of New York (Kendeigh, 1946), and beech-maple-pine of northern lower Michigan (Kendeigh, 1948). Weights for each species are taken from the literature for the locality nearest the area studied. Since in all of these reports densities of some birds are given as either plus or minus, a value of ½ bird per 100 acres was assigned to plus and ¼ to minus densities. The results of the calculations are given in table 10 and in figures 2 to 4. In the beech-maple-hemlock succession, biomass values have been calculated separately for the early, middle, and late facies of the avifauna of the mixed shrubs and small trees stage. In the Michigan report, data from two successional sequences are

given; grassland-aspen-pine on the upland and cedar-aspen and cedar-balsam on the bogs. Both sequences lead to the same climax of beech-maple-pine. The two lines of succession are shown in the graph.

DESCRIPTION OF CENSUS AREAS

CONIFEROUS VEGETATION-TYPES

Lodgepole (table 2).—The lodgepole census area was at the northwest end of String Lake below the south shoulder of Indian Paintbrush Canyon at an elevation of 6900 feet. Near the lake the area is relatively flat but the slope becomes progressively greater

Table 2

Lodgepole Pine

(Distance, 0.49 miles; area, 10 acres; number of counts, 6)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	0.67	6.7	13.1	88	41
Western Tanager (*Piranga ludoviciana*)	0.50	5.0	29.0	145	53
Totals				233	94
Foliage-Seed					
Canada Jay (*Perisoreus canadensis*)	0.30	3.0	74.6	224	62
Clark Nutcracker (*Nucifraga columbiana*)	0.17	1.7	130.0	221	51
Siskin (*Spinus pinus*)	0.17	1.7	12.1	1	10
Totals				466	123
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	0.67	6.7	12.0	80	38
Totals				80	38
Ground-Insect					
Chipping Sparrow (*Spizella passerina*)	0.17	1.7	12.2	21	10
Totals				21	10
Ground-Seed					
Oregon Junco (*Junco oreganus*)	1.00	10.0	17.7	177	75
Totals				177	75

toward the base of the mountain to the west. The canopy vegetation is an almost pure stand of even-aged lodgepole pines (*Pinus contorta*) forty to sixty feet high, spaced three to twelve feet apart. Only the top branches of the trees carry needles. Most of the space below this thin canopy is filled by scaffoldwork of bare trunks hung with dead branches. There are a few dead aspens (*Populus tremuloides*) standing in the forest and both fallen aspens and lodgepoles on the ground. The understory consists of scattered seedlings of alpine firs (*Abies lasiocarpa*) three to six feet high and a nearly continuous ground cover of *Lupinus* and grasses interrupted by *Lonicera* and *Vaccinium* bushes. There are a few large boulder outcrops, and the soil appears to be thin.

Lodgepole-spruce-fir (table 3).—This transect area was on the south shoulder of

Indian Paintbrush Canyon at an elevation of 7300 feet. The overstory vegetation is a mixture of three species; lodgepole pine, Engelmann spruce (*Picea engelmannii*), and alpine fir (*Abies lasiocarpa*); it is not, however, a uniform mixture. Rather, where the transect begins, lodgepole pine predominates with only a few spruce and fir present. Along the transect route spruces and firs gradually become more frequent so that where the transect ends they outnumbered the lodgepoles. Generally the trees are slender, 6 to 12 inches (d.b.h.) and closely spaced. To some degree the lodgepoles and generally the spruces and firs have some needles on the branches below the tops of the trees so that the canopy layer is thicker than in pure lodgepole forest. The understory is a somewhat sparse but continuous layer of shrubs—*Lonicera, Vaccinium, Ribes, Sorbus* and *Spirea* —except where rock outcrops exist or a windfall has made an opening in the forest. In these places grasses and smaller forbs such as *Lupinus* are more common. There are a

Table 3

Lodgepole-Spruce-Fir

(Distance, 0.85 miles; area, 15 acres; number of counts, 12)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	2.75	18.3	13.1	240	112
Western Tanager (*Piranga ludoviciana*)	2.75	18.3	29.0	531	193
Ruby-crowned Kinglet (*Regulus calendula*)	1.42	9.4	6.1	57	33
Golden-crowned Kinglet (*Regulus satrapa*)	0.25	0.6	5.1	3	2
Totals				831	340
Foliage-Seed					
Clark Nutcracker (*Nucifraga columbiana*)	1.75	11.7	130.0	1521	351
Pine Grosbeak (*Pinicola enucleator*)	0.08	0.6	51.0	31	9
Totals				1552	360
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	1.17	7.8	12.0	94	44
Red-breasted Nuthatch (*Sitta canadensis*)	0.50	3.3	10.1	33	17
Creeper (*Certhia familiaris*)	0.08	1.1	8.0	9	5
Totals				136	66
Timber-Drilling					
Hairy Woodpecker (*Dendrocopos villosus*)	0.25	1.7	69.8	119	33
Totals				119	33
Ground-Insect					
Chipping Sparrow (*Spizella passerina*)	1.67	11.1	12.2	135	64
Robin (*Turdus migratorius*)	0.33	2.2	88.0	194	51
Totals				329	115
Ground-Seed					
Oregon Junco (*Junco oreganus*)	1.42	9.4	17.7	166	71
Cassin Finch (*Carpodacus cassinii*)	0.33	2.2	27.6	61	22
Totals				227	93

good many dead trees present; many are tangled with living trees and remain propped upright.

Spruce-fir (table 4; fig. 1).—The transect was made in a forest of Engelmann spruce and alpine fir containing some Douglas fir (*Pseudotsuga taxifolia*). It is on the south side of Indian Paintbrush Canyon near the mouth and at a slightly higher elevation,

Table 4

Spruce-Fir

(Distance, 0.7 miles; area, 13 acres; number of counts, 11)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Olive-sided Flycatcher (*Nuttallornis borealis*)	0.18	1.4	31.5	44	16
Totals				44	16
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	1.00	7.7	13.1	101	47
Western Tanager (*Piranga ludoviciana*)	1.73	13.3	29.0	386	140
Ruby-crowned Kinglet (*Regulus calendula*)	1.09	8.4	6.1	51	29
Golden-crowned Kinglet (*Regulus satrapa*)	1.54	11.9	5.1	61	37
Totals				599	253
Foliage-Seed					
Clark Nutcracker (*Nucifraga columbiana*)	2.64	20.3	130.0	2639	609
Pine Grosbeak (*Pinicola enucleator*)	0.45	3.5	51.0	179	55
Siskin (*Spinus pinus*)	0.18	1.4	12.1	17	8
Totals				2835	672
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	0.91	7.0	12.0	84	40
Creeper (*Certhia familiaris*)	0.55	4.2	8.0	34	18
Red-breasted Nuthatch (*Sitta canadensis*)	0.45	3.5	10.1	35	18
Totals				153	76
Timber-Drilling					
Hairy Woodpecker (*Dendrocopos villosus*)	0.36	2.8	69.8	195	55
Arctic Three-toed Woodpecker (*Picoides arcticus*)	0.09	0.7	73.2	51	14
Totals				246	69
Ground-Insect					
Robin (*Turdus migratorius*)	0.45	3.5	88.0	308	80
Chipping Sparrow (*Spizella passerina*)	0.36	2.8	12.2	34	16
Hermit Thrush (*Hylocichla guttata*)	0.45	3.5	25.6	90	34
Swainson Thrush (*Hylocichla ustulata*)	0.36	2.8	30.0	84	30
Totals				516	160
Ground-Seed					
Oregon Junco (*Junco oreganus*)	0.91	7.0	17.7	124	53
Cassin Finch (*Carpodacus cassinii*)	0.18	1.4	27.6	39	14
Totals				163	67

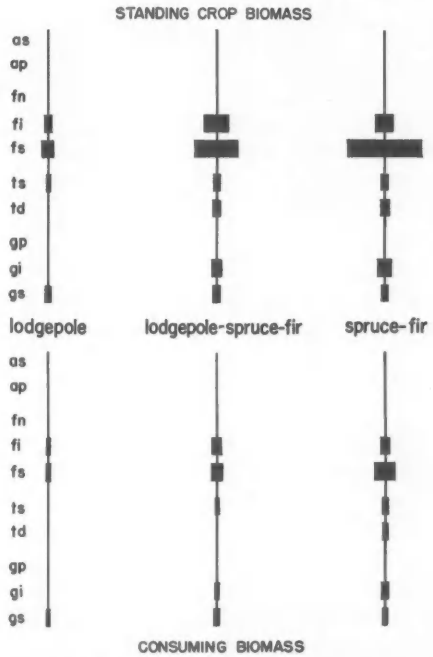

Fig. 2. Diagram of biomass values of the avifaunas of the three coniferous forest communities. The total length of each bar is proportional to the biomass in grams. For abbreviations, see table 8, and for actual biomass values, see tables 2, 3, and 4.

7600 feet, than the previous transect. The trees are large and mature, forming a semi-closed canopy sixty to one hundred feet from the ground. The canopy is locally interrupted by openings resulting from rock outcrops or windfalls. Moss grows on the tree trunks. The understory is a mixture of leafy shrubs: *Vaccinium, Lonicera, Rubus, Ribes* and *Amelanchier*. Seedlings of the dominant trees are also present. There is a fairly thick layer of duff over the ground in most places, and large boulders, some eight to ten feet in diameter, protrude through the understory. Several small streams cross the transect, and in one place the transect parallels the river of the canyon.

It seems reasonable to postulate that these three vegetation-types represent two successional stages plus an intermediate mixture of the series for this location. One is led to this view by seeing that alpine fir is replacing the lodgepole forest in transect 1. Furthermore, in transect 3 the Engelmann spruce, alpine fir and Douglas fir are all replacing themselves. All three communities stand on the same soil (Fryxell, 1930), namely glacial moraine composed chiefly of gneiss derived from parent material higher in the canyon itself.

DECIDUOUS VEGETATIONS

Willow-sedge swamp (table 5; fig. 1).—A floristic description of this vegetation is given by Reed (1952). The transect ran parallel to the dirt road between the Biologi-

Table 5

Willow-Sedge Swamp

(Distance, 0.5 miles; area, 10 acres; number of counts, 6)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	5.17	51.7	12.7	657	305
Western Wood Pewee (*Contopus richardsonii*)	0.33	3.3	14.0	46	22
Totals				703	327
Foliage-Nectar					
Calliope Hummingbird (*Stellula calliope*)	4.33	43.3	2.5	108	82
Totals				108	82
Foliage-Insect					
Yellow Warbler (*Dendroica aestiva*)	10.17	101.7	9.7	986	498
Yellow-throat (*Geothlypis trichas*)	5.17	51.7	10.0	517	259
Tolmie Warbler (*Oporornis tolmiei*)	1.00	10.0	11.4	114	55
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.17	1.7	46.0	78	25
Totals				1695	837
Timber-Drilling					
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.67	6.7	45.2	303	96
Totals				303	96
Ground-Insect					
Robin (*Turdus migratorius*)	2.17	21.7	88.0	1910	499
Wilson Snipe (*Capella delicata*)	1.17	11.7	100.0	1170	294
Fox Sparrow (*Passerella iliaca*)	2.00	20.0	30.6	612	218
Lincoln Sparrow (*Melospiza lincolnii*)	6.50	65.0	17.5	1138	481
Swainson Thrush (*Hylocichla ustulata*)	0.67	6.7	30.0	201	72
Totals				5031	1564
Ground-Seed					
White-crowned Sparrow (*Zonotrichia leucophrys*)	1.50	15.0	28.5	428	156
Song Sparrow (*Melospiza melodia*)	3.00	30.0	21.0	630	252
Totals				1058	408

cal Station and the Jackson Lake Ranger Station on U. S. Highway 26 and 287. The Biological Station is 0.8 miles west of Moran at B.M. 6750. The vegetation consists of an irregular cover of low willows two to four feet high between which grow sedges and grasses. Within the low willow area are groves of large willows ten to twelve feet high. The groves are frequently "hollow" or circular with a stand of lush grass in the middle. Along the stream courses are willows six to ten feet high in a continuous cover. Moose trails criss-cross through the swamp as do the moose themselves at evening. During early summer the soil is saturated with water and forms a dark muck.

Scrub-meadow (table 6).—This transect was made in a mountainside area below

Table 6

Scrub-Meadow

(Distance, 0.1 miles; area, 2 acres; number of counts, 10)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	0.2	10.0	12.7	127	59
Totals				127	59
Foliage-Nectar					
Broad-tailed Hummingbird (*Selasphorus platycercus*)	0.9	45.0	4.0	180	117
Totals				180	117
Foliage-Insect					
Warbling Vireo (*Vireo gilvus*)	1.2	60.0	11.3	678	330
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.9	45.0	46.0	2070	657
Tolmie Warbler (*Oporornis tolmiei*)	1.7	85.0	11.4	969	468
Yellow-throat (*Geothlypis trichas*)	0.1	5.0	10.0	50	25
Totals				3767	1480
Ground-Insect					
Swainson Thrush (*Hylocichla ustulata*)	1.0	50.0	30.0	1500	540
Lincoln Sparrow (*Melospiza lincolnii*)	1.0	50.0	17.5	875	370
Chipping Sparrow (*Spizella passerina*)	0.6	30.0	12.2	366	173
Robin (*Turdus migratorius*)	0.3	15.0	88.0	1320	345
Totals				4061	1428
Ground-Seed					
Oregon Junco (*Junco oreganus*)	0.7	35.0	17.7	620	263
Lazuli Bunting (*Passerina amoena*)	1.0	50.0	15.0	750	333
Song Sparrow (*Melospiza melodia*)	0.5	25.0	21.0	525	211
White-crowned Sparrow (*Zonotrichia leucophrys*)	0.7	35.0	28.5	998	364
Totals				2893	1171

Rockchuck Peak on the shoulder of Indian Paintbrush Canyon at an elevation of 7300 feet. The vegetation is the product of two principal influences: the small streams which run down the face of the peak through the region and keep the soil moist through the first half of the summer, and periodic avalanches in the winter and spring which subject the vegetation to repeated onslaughts. As a result the area is covered by a scrub of small aspens, some only two or three feet high and others five to ten feet high. All are bent downhill. Dominant with the aspens are shrubs such as *Ceanothus*, *Lonicera*, and *Prunus* and numerous forbs and grasses. In the moister portions are willow groves six feet high and larger aspens. Where there is a small level area the soil is deeper and a small grassy meadow is formed. Around the margins of the snowtrack, Engelmann spruce and alpine fir grow. Similar snowtrack scrub areas, frequently dominated by willows, are found throughout the canyons of the Tetons wherever the slope is too great to hold the snowpack through the winter.

Flatland aspen (table 7; fig. 1).—The censuses were made in a series of contiguous aspen groves along the west bank of the "Snake-Knee" 0.6 miles east of the Biological Station. Each grove is a cluster, some "hollow," of aspens forty to seventy feet high. The center of the grove, if hollow, has many downed logs. The groves form a leafy open

Table 7

Flatland Aspen

(Distance, 0.3 miles; area, 6 acres; number of counts, 5)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Soaring					
Tree Swallow (*Iridoprocne bicolor*)	28.0	467.6	20.0	9352	3787
Totals				9352	3787
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	2.6	43.4	12.7	551	256
Western Wood Pewee (*Contopus richardsonii*)	1.0	16.7	14.2	237	107
Totals				788	363
Foliage-Nectar					
Calliope Hummingbird (*Stellula calliope*)	0.8	13.4	2.5	34	25
Totals				34	25
Foliage-Insect					
Yellow Warbler (*Dendroica aestiva*)	7.6	126.9	9.7	1231	622
Tolmie Warbler (*Oporornis tolmiei*)	1.8	30.1	11.4	343	165
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1.2	20.0	46.0	920	292
House Wren (*Troglodytes aedon*)	1.4	23.4	10.5	246	121
Warbling Vireo (*Vireo gilvus*)	0.8	13.4	11.3	151	73
Totals				2891	1273
Timber-Drilling					
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3.0	50.1	45.2	2265	721
Totals				2265	721
Ground-Insect					
Flicker (*Colaptes cafer*)	3.2	53.4	145.0	7743	1736
Mountain Bluebird (*Sialia currucoides*)	1.8	30.1	26.6	801	299
Robin (*Turdus migratorius*)	1.8	30.1	88.0	2649	692
Lincoln Sparrow (*Melospiza lincolnii*)	3.2	53.4	17.5	935	395
Chipping Sparrow (*Spizella passerina*)	0.8	13.4	12.2	163	77
Totals				12291	3199
Ground-Seed					
White-crowned Sparrow (*Zonotrichia leucophrys*)	2.4	40.1	28.5	1143	418
Oregon Junco (*Junco oreganus*)	0.4	6.7	17.7	119	50
Song Sparrow (*Melospiza melodia*)	0.4	6.7	21.0	141	57
American Goldfinch (*Spinus tristis*)	0.4	6.7	12.0	80	38
Totals				1483	563

canopy. Below the canopy the ground is covered with a lush tangle of shrubs; *Epilobium, Potentilla, Geranium* and other shrubs as well as grasses and flowering herbs are present. Insects are abundant and the ground is usually moist.

Hillside aspen.—The transect in hillside aspens was made in a grove on the south-facing slope just north of Highway 26 and 287, 1.7 miles east of Jackson Lake Ranger Station. The elevation is about 6900 feet. In aspect it is a continuous stand of fairly closely spaced slender aspens twenty to forty feet high. The understory is a thick rank growth of shrubs and grasses with many fallen aspen trunks. Superficially these groves

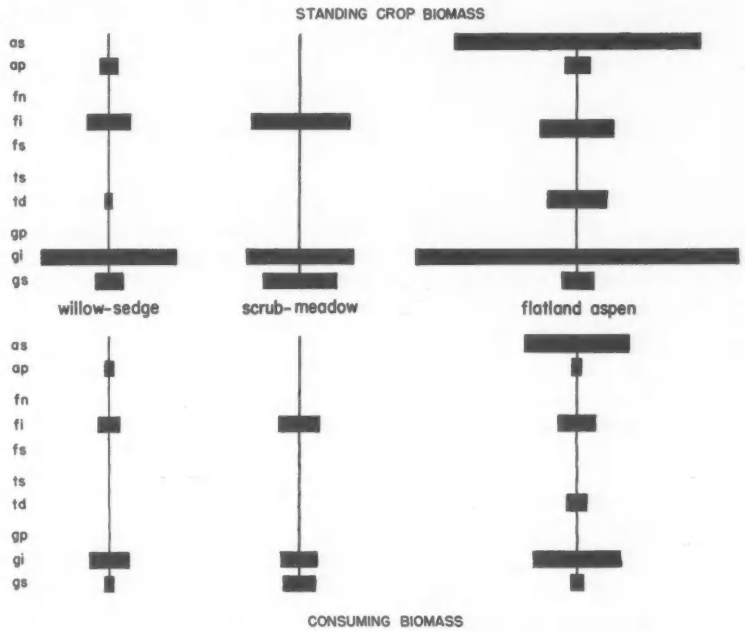

Fig. 3. Diagram of biomass values of the avifaunas of the three deciduous vegetation communities. For explanation, see figure 2. For actual biomass values, see tables 5, 6, and 7.

appear similar to those of the flatland aspen, but Reed's analysis demonstrates that there are fewer plant species composing the understory vegetation. No census data are given for this transect in the tables, but comments on the avifauna will be made in the discussion.

DISCUSSION

From the data in the tables and diagrams, certain inferences can be made about trophic or feeding relationships and community structure. However, before discussing these points it is important to call attention to the relationship between size of bird and required food intake. Large birds consume less oxygen and hence require less food per gram of body weight than small birds (Benedict, 1938; Brody, 1945). It follows that, from a community standpoint, a larger standing crop can be maintained on the same energy supply with large birds than with small ones. Also, large birds are not so sensi-

tive to short term fluctuations in the food supply (Kendeigh, 1945). If two birds, alike in other respects, have ten per cent of their body weight present as stored food, a bird of 50 grams, for example, will last 1.6 times as long without food under a given set of conditions as a bird of 10 grams. Large size is not an unmixed blessing, however; a large bird eats more than a small one. Like all birds, they require that their food items be concentrated enough in location or present in large enough pieces so that they gain more energy from the food than they expend in gathering it.

Were the size-food requirement the only force operating, the avifauna would come to be entirely large birds. What brings about, then, the inclusion of small birds in an avifauna? It seems likely that natural selection acting on individuals of each species exerts a selection on the structure of the ecosystem to produce the most efficient utilization of the energy available under a given set of conditions (Allee, *et al.*, 1949: 695–729). Under this selective pressure no energy source remains unexploited for long. Much of the energy of the community is trapped in small particles of matter such as seeds, egg masses of spiders, scale insects and the like. Since only a small bird having specialized feeding apparatus and habits can gather these small particles efficiently, the avifauna comes to be composed of birds of a variety of sizes corresponding to the feeding niches available. But within each feeding niche the advantage of larger size still operates, and it would appear that each species tends toward the largest size that its feeding procedures will permit.

These relationships play an important role in determining avifaunal structure of a community as will be illustrated in the remarks which follow.

The three coniferous forest types, for reasons already given, I regard as successional stages in a series, lodgepole pine being earliest and spruce-fir latest. It is apparent when one walks through these three forests that from the lodgepole to the spruce-fir there is a progressive increase in green leaf surface. The canopy in the spruce-fir forest is thicker and more nearly complete and the forest floor is in darker shade. At the same time the plant understory is more complete than in the lodgepole forests. It seems evident that the spruce-fir forest is trapping a larger amount of solar energy and that the flow of energy through the community is therefore greater than through the lodgepole forest.

In the avifaunas of these forests parallel differences exist as can be seen in the tables and diagram. As succession proceeds from the lodgepole stage to the spruce-fir stage, the number of species of birds in the avifauna increases. A similar increase has been found in other successions (Kendeigh, 1946, 1948; Odum, 1950; Johnston and Odum, 1956). Moreover, the increase is not an increase in the number of species feeding in the canopy and a decrease in the birds feeding on the ground but an increase in all categories. These changes may be interpreted as reflecting the increase in complexity of the vegetation. The changes suggest that in early seral stages only sufficient food energy is present in a given stratum or feeding category to support a few generalized species. As the community matures, enough energy flows through the stratum so that it may be partitioned between a number of specialized species. When this happens, one may presume that the generalized species, if they are to remain in the avifauna, are forced by competition to adopt more specialized feeding habits themselves.

Not only does the number of species increase but the biomass values also increase from early to late successional stage. Standing crop biomass increases by over four times and consuming biomass by nearly that much.

There is a change in the ratio of consuming biomass to standing crop biomass from early to later successional stage (table 8). In the lodgepole avifauna it is 0.35, in the lodgepole-spruce-fir 0.32, and in the spruce-fir 0.29, a progressive and regular decrease in this ratio. This means that there is a progressive increase in the percentage of the bio-

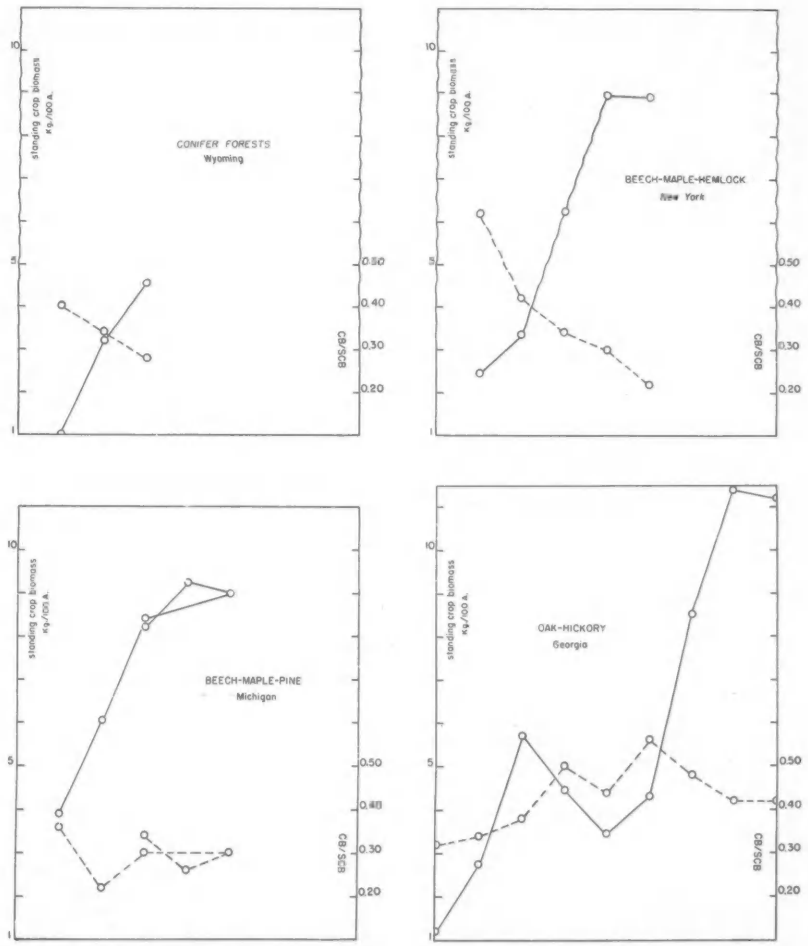

Fig. 4. Graphs of avian standing crop biomasses (solid line) and consuming biomass-standing crop biomass ratios (broken line) in stages of the Wyoming coniferous forest, beech-maple-hemlock, beech-maple-pine, and oak-hickory successions. Stages of each succession are plotted as abcissae.

mass of the avifauna present as larger species. Applying the generalizations discussed above, it becomes evident that the later successional stage is supporting a larger biomass on a given energy budget than is the earlier stage. The avifauna of spruce-fir community then can be said to have not only a greater energy flow through it but a greater efficiency in utilizing this energy.

Censuses of birds are known to have high variances regardless of the methods employed (Dice, 1952:76–78), so it is well to be cautious in generalizing from such data.

Table 8

Biomass Values per 100 Acres, and Ratios

	Standing crop biomass, grams	Consuming biomass, grams	Ratio
Lodgepole pine, table 2			
Primary consumers G-S, F-S	643	198	
Secondary consumers G-I, T-S, F-I	334	142	
Totals and ratio	977	340	0.35
Lodgepole-spruce-fir, table 3			
Primary consumers G-S, F-S	1779	453	
Secondary consumers G-I, T-D, T-S, F-I	1415	554	
Totals and ratio	3194	1007	0.32
Spruce-fir, table 4			
Primary consumers G-S, F-S	2998	739	
Secondary consumers G-I, T-S, T-D, F-I, A-P	1558	574	
Totals and ratio	4556	1313	0.29
Willow-sedge swamp, table 5			
Primary consumers G-S, T-D, F-N	1469	586	
Secondary consumers G-I, F-I, A-P	7429	2728	
Totals and ratio	8898	3314	0.37
Scrub-meadow, table 6			
Primary consumers G-S, F-N	3073	1288	
Secondary consumers G-I, F-I, A-P	7955	2967	
Totals and ratio	11028	4255	0.39
Flatland aspen, table 7			
Primary consumers G-S, T-D, F-N	3782	1309	
Secondary consumers G-I, F-I, A-P, A-S	25322	8622	
Totals and ratio	29104	9931	0.34

Abbreviations: A-S, air-soaring; A-P, air-perching; F-N, foliage-nectar; F-I, foliage-insect; F-S, foliage-seed; T-S, timber-searching; T-D, timber-drilling; G-I, ground-insect; G-S, ground-seed.

But two of the graphs, that of the beech-maple-hemlock of New York and the beech-maple-pine of Michigan show the same consistent increase in standing crop biomass from early to late stage as is shown by the Wyoming graph, and the graph of the oak-hickory of Georgia shows the same general trend with a sharp dip in the middle. Whatever the interpretation of the entire trend of the Georgia graph, the trend in the latter half of the succession is consistently upward. It seems quite reasonable to conclude,

then, that we may expect to find in a great many successions an increase in standing crop biomass from early to late seral stages. This parallels the increases in numbers of species of birds and of individuals which we have come to expect from earlier studies.

The trend in the value of the ratio of consuming biomass to standing crop biomass is really of more fundamental import than the standing crop biomass. Remembering that the efficiency in energy utilization of the avifauna of a community is concluded to

Table 9

Numbers of Species

Feeding category	Vegetation-type: Lodge-pole	Lodgepole-spruce-fir	Spruce-fir	Willow-sedge	Scrub-meadow	Flatland aspen
Air-Soaring	....	....	....	....	....	1
Air-Perching	....	....	1	2	1	2
Foliage-Nectar	....	....	....	1	1	1
Foliage-Insect	2	4	4	4	4	5
Foliage-Seed	3	2	3	....	....	....
Timber-Searching	1	3	3	....	....	....
Timber-Drilling	....	1	2	1	....	1
Ground-Insect	1	2	4	5	4	5
Ground-Seed	1	2	2	2	4	4
Totals	8	14	19	15	14	19

be inversely proportional to this value, a declining value or slope should be read as indicating an increase in efficiency. We have already noted that such an increase in efficiency can be seen in the Wyoming coniferous succession. In the successions from the eastern United States a similar increase in efficiency can be seen clearly in the beech-maple-hemlock of New York, an initial high efficiency followed by a decline and then a rise in efficiency in the later stages in the Georgia succession and an irregular pattern of values in the succession in Michigan which might possibly be interpreted as showing a slight overall increase in efficiency, although it does very little to support a generalization one way or another.

From the graphs it is possible to say that frequently succession in avifaunas will show an increase in efficiency with seral progression, the avifauna of the climax community being the most efficient in energy utilization.

Parenthetically, an illustration of the value of this type of study in community ecology may be inserted. While I was in Wyoming I heard plant ecologists debating whether the alpine fir-Engelmann spruce forest was the climax vegetation of the Teton canyons or not. Now, it will be noticed that in the graphs of the eastern successions the subclimax has a standing crop biomass that is nearly as great as or is greater than that of the climax. By analogy then, one might argue that the spruce-fir is probably not the climax but the subclimax. The climax is perhaps some other community which has been removed either by lumbering or fire, possibly Douglas fir, as some botanists believe.

It will be noticed that in the avifaunas of the coniferous forests the biomass of primary consumers or herbivores exceeds that of the secondary consumers or carnivores while in the deciduous forest avifaunas just the reverse relationship exists. This would seem to be a significant and fundamental difference between these two types of avifaunas. However, no such relationship seems to exist in the examples from the eastern United States, so there is no way of assessing the importance of this observation until more information from other areas becomes available.

The three deciduous vegetation communities do not stand in any relationship to one

another in succession. They are in fact very likely to be members of different successional series. The flatland aspen and willow-sedge swamp communities are both on soil the parent material of which is outwash or till from Pinedale glaciers from the north. The principal constituent is quartzite, whereas the scrub-meadow community is on the same gneiss-dominated moraine soil as are the coniferous forest communities. All three communities have high ground moisture, especially the swamp which is covered with water during the early summer. In spite of these differences, the structures of the vegeta-

Table 10

Avifaunal Characteristics of Three Successions of the Eastern United States*

Beech-maple-hemlock, New York (Kendeigh, 1946)

	Mixed shrubs and small trees			Hemlock-beech	Beech-maple-hemlock
	Early	Middle	Late		
Standing crop biomass, gms.	2451*	3347	6255	8967	8902
**CB/SCB ratio	0.46	0.36	0.32	0.30	0.26

Beech-maple-pine, Michigan (Kendeigh, 1948)

	Grass-land	Aspen-red maple	Pine-aspen	Cedar-aspen	Cedar-balsam	Beech-maple-pine
Standing crop biomass, gms.	3930	6038	8405	8238	9249	8989
CB/SCB ratio	0.33	0.26	0.30	0.32	0.28	0.30

Oak-hickory, Georgia (Johnston and Odum, 1956)

	Grass-forb		Grass-shrub		Pine forest				Oak-hickory
	1	2	1	2	1	2	3	4	
Standing crop biomass, gms.	1210	2742	5703	4453	3460	4317	6582	11419	11215
CB/SCB ratio	0.31	0.32	0.34	0.40	0.37	0.43	0.39	0.36	0.36

* Quantities expressed on basis of 100 acres for each community.
** Consumer biomass-standing crop biomass ratio.

tion of the willow-sedge swamp and the mountainside scrub-meadow communities are very similar. Although the numbers of species in the two avifaunas are nearly the same, the willow-sedge swamp avifauna shows slightly more diversity into different niches and a lower ratio of consumer biomass to standing crop biomass and hence higher efficiency.

The standing crop biomass for the flatland aspen avifauna is certainly too large. Many of the birds in those groves, such as robins and flickers, do a considerable part of their feeding outside the groves. It is impossible to estimate what percentage of their energy comes from outside the groves, but even if the value for the standing crop biomass for the whole avifauna were cut in half, it would still be a figure comparable in size with those for the two other deciduous-vegetation communities.

We may compare this figure with that of the hillside aspen groves. It was mentioned earlier that these groves appear superficially similar to some of the flatland groves, and one might infer that many of the same niches should be present. These hillside groves, because of soil characteristics and slope are drier than the flatland groves. Furthermore, the two types "differ markedly from a floristic point of view" (Reed, 1952:710). The hillside community shows a much less varied flora than that of the flatland, having only about half the number of shrubs, forbs, and grasses. It seems likely that the metabolic

efficiency of the hillside groves is also less than that of the flatlands, although it would not be obvious from their appearance. Significantly the avifauna also is impoverished, in fact more markedly than the flora. I found the following species established in the hillside grove: Warbling Vireo, Lazuli Bunting, Black-headed Grosbeak, Western Tanager, Audubon Warbler (doubtful), Yellow-bellied Sapsucker, and Western Wood Pewee. In counts on a transect of the same size as that in the flatland aspen the maximum number of individuals found of all species combined was fourteen; more often it was five to ten. When compared with the flatland groves, the difference is impressive. The avifaunas appear not only to respond in the same way as the plants to the two sets of conditions, but in an even more extreme manner.

It now remains to combine all the relationships discussed into a unified statement regarding avifaunas and their place in the communities of which they form a part. The community in the sense of an ecosystem undergoes a series of integrated changes as succession proceeds toward the climax. The avifaunal constituent of the community participates in these changes in a regular and apparently predictable pattern. This pattern consists of the following increases: numbers of species, reflecting an increase in diversity of habitat; numbers of individuals; standing crop biomass; and, in the latter stages of the succession, greater efficiency and stability of the avifauna judged by its utilization of the energy resources of the community. The highest standing crop biomass occurs in either the subclimax or climax. The energy flow through the avifauna, as indicated by consuming biomass, increases from early to later stages.

The avifauna is a constituent of the community integrated with the rest of the ecosystem in development during succession. The question now arises as to how close this integration is. Does the avifauna parallel precisely or nearly precisely the development in energy utilization of the entire ecosystem? If it does, then a measure of the energy metabolism of the avifauna will provide an index of the metabolism of the entire community to be used for comparisons between stages in the succession and between ecosystems. There is not nearly enough information available now to form a basis for an answer to this question. Palmgren (1928) found that in the avifaunas of the forests of Finland the number of birds was greater in the more productive forest-types. In Wyoming, the consuming biomass of the avifaunas increases with community succession in the coniferous forests and parallels soil and vegetation characteristics in the aspen groves. All of these circumstances suggest that a relationship probably exists between avifaunal biomass and community energy utilization.

SUMMARY

Censuses by strip transect of bird populations in six vegetation types at Jackson Hole, Wyoming, have been made. The three coniferous vegetation types are lodgepole, lodgepole-spruce-fir, and spruce-fir. These three are regarded as a successional sequence. The three deciduous forest types are willow-sedge swamp, scrub-meadow, and flatland aspen.

The avifauna of each community has been analyzed into categories on the basis of feeding habits. Standing crop biomasses (total weight of living material) for each category and avifauna have been calculated. A consuming biomass of an avifauna is defined as the sum of species consuming biomasses. These are calculated by multiplying number of individuals times the mean weight of the species to the 0.7 exponent. Grams of consuming biomass are regarded as equivalent in terms of food consumption regardless of size of species. Total consuming biomass is taken as an index to energy metabolism by an avifauna. The efficiency of a species in energy use is proportional to its size. As a product of this relationship, the efficiency of an avifauna is indicated by the proportion

of its biomass made up of large birds. This value is measured by the ratio of consuming biomass to standing crop biomass. The smaller the value, the greater is the efficiency.

In the coniferous forest avifaunas an increase has been found in standing crop biomass and in efficiency, as measured by the ratio of consuming biomass to standing crop biomass, as succession proceeds toward the climax. Similar relationships have been found in the avifaunas of three successions of the eastern United States reported in the literature: oak-hickory of Georgia, beech-maple-hemlock of New York, and beech-maple-pine of Michigan.

In the avifaunas of Jackson Hole those of the coniferous forest have a greater herbivore (primary consumer) biomass than they do carnivore (secondary and tertiary consumer) biomass. In the deciduous forest avifaunas the relationship is reversed.

Willow-sedge swamp and scrub-meadow avifaunas of Jackson Hole are of about equal standing crop biomass, but that of the willow-sedge swamp is more diversified, having more species in more categories.

The avifaunas of the aspen groves parallel in a magnified way, in their species composition and biomasses, differences in floristics of hillside aspen and flatland aspen groves. Hillside aspen groves, which have about half the number of species of plants present in flatland groves, also have a meager avifauna. The avifauna of the flatland groves is rich and varied and has a large standing crop biomass.

It is suggested that avifaunal size and efficiency in energy metabolism may prove to reflect ecosystem functions accurately enough so that avifaunal characteristics may be used as indices of the metabolism and efficiency of the entire biotic community.

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AVIAN ANATOMY AND THE ANATOMIST

By M. JOLLIE

Berger (1956*a*) summarized the anatomical variations found in man in four areas of study, namely neurology, myology, osteology, and angiology, with the purpose of demonstrating the kinds of variation to be expected and evaluated in birds. I would like to discuss the obvious, additional category, variations attributable to the anatomist and not to the anatomy of the subject.

An example of an area of disagreement in interpretation is supplied by the description of the muscle known as the "expansor secundariorum" of the pigeon presented by Berger (1956*b*). The "expansor secundariorum" is an extremely difficult structure to study, lying as it does embedded in the subcutaneous connective tissue and associated in part with the strong bracing connective tissue behind and within the axilla of the wing. I am of the opinion that most anatomists have preferred not to describe this area; therefore, it is with considerable hesitation that I attempt to alter the present concepts.

I can agree with Berger that sometimes there are two structures involved in this complex. Occasionally there is a minute muscle belly which, as in the pigeon, *Columba livia* (fig. 1), arises off the connective tissue band from the axilla and inserts in common with the triceps. This muscle is properly, as suggested, a part of the triceps; it can be identified as the pars axillaris. The main "muscle" is a part of a complex or series which is not clearly understandable in terms of Berger's description, in which it is assumed that the muscle fibers associated with the axillary tendon form the belly of a skeletal muscle.

Before discussing the muscle let us consider its "tendon," which may be but one band within the connective tissue of this area. This connective tissue has the function of holding the skin tightly to the base of the wing. Fibers extend out to the skin from the region of insertion of the latissimus dorsi and also from behind the shoulder joint and from the strong connective tissue enclosing the axillary nerves and blood vessels. Within the axillary mass, and sometimes dorsally, small bands frequently can be detected and occasionally these are continuous with the "tendon" described for the "expansor secundariorum." Even when such a "tendon" is lacking, a "vestigial" attachment may be observed in the axilla. Dorsally there may be a strong connective tissue brace for the humeral (better called scapular) tract of feathers.

The relationship between the muscle fibers of the "expansor secundariorum" and the band of connective tissue from the axilla is a direct one, since this band is a functional response to the need for anchorage of a part of this muscle complex (therefore not really in disagreement with Fürbringer, 1902:575). This band may be used in the origin of other parts; it may be an important area of origin. The configuration of the base of the wing apparently determines whether an axillary connective-tissue band is needed.

Because of its erratic functional nature and because it is not associated primarily with a skeletal muscle, this band is not properly a tendon. It might best be called a secondary tendon or brace. In the case of the passerines (fig. 2) the axillary accessory is replaced by a marginal one. The explanation may be that the dorsal brace to the scapular (humeral) tract functionally replaces the more ventral one. The axillary "tendon" is not a vestige of a once better developed muscle; it is a specialization in those species where it occurs.

The muscle fibers in question are modified from those associated with the feathers; these are typically diagonally disposed. The "expansor secundariorum" is made up of a well-developed group of such feather muscles which serves two purposes: (1) depres-

sion of the secondaries and tertiaries (that is, it resists their upward displacement in flight) and (2) drawing them medially so as to increase the support area of the inner wing. The depressors of the secondaries arise off the thickened fascia of the posterior ventral margin of the wing; medially this is anchored to the distal end of the humerus (or the humeroulnar ligament) and braced in the pigeon by the tendon-like band from the axilla. The depressors become weaker as one proceeds distally along the ulna four or five secondaries. There is a smaller series of antagonistic dorsal muscles for the secondaries and their coverts.

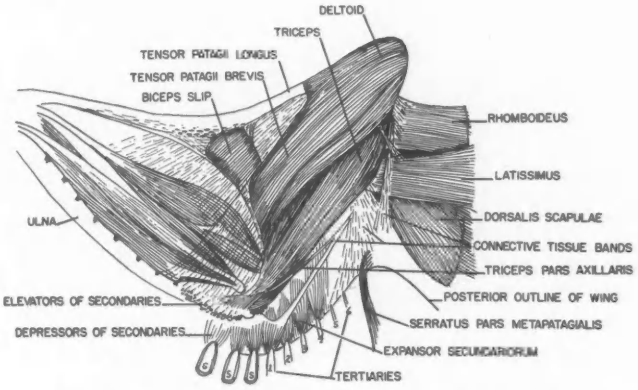

Fig. 1. Dorsal view of dissected wing of the pigeon, *Columba livia*

The description (and figures) of the expansor secundariorum of the Crow (*Corvus brachyrhynchos*) by Hudson and Lanzillotti (1955) does not apply to the Raven (*Corvus corax*). In this latter species (fig. 2) there is no axillary band but there is one which extends from the fibers of the depressor-adductors of the tertiaries to the posterior end of the scapular (humeral) tract of feathers (at the insertion of the pars metapatagialis of the serratus muscle). This same area is braced by connective tissue extending back from the axilla and from the shoulder area in general.

The marginal connective tissue band of the metapatagium lies below the quills of the tertiaries and is continuous with their sheaths. Midway toward the elbow, muscle fibers arise off the skin and from this band; these insert in part on the connective tissue sheaths of the inner tertiary quills. Many of the fibers parallel the line of the band and continue to the area just before the elbow where they insert on the quills of the outer tertiaries and the inner secondaries. Hudson and Lanzillotti (*op. cit.*:23) have described the remainder of this series, that is, the depressor fibers of the secondaries. The dorsal elevators of the secondaries are very weakly developed in the Raven.

Berger (1956*b*:153) has pointed out that the "expansor secundariorum" is composed of smooth muscle fibers while those of the humeral or forearm origin, which depress the secondaries, are striated. Whether a muscle is smooth or striated is dependent in part on its function. The assumption that the depressors of the secondaries are part of the "M. flexor carpi ulnaris" will have to be demonstrated although this is a possibility.

Another example of difference in interpretation is supplied by description of the pec-

toralis as double or single, that is, the pectoralis of the Whooping Crane (*Grus americana*) is described by Fisher and Goodman (1955:45), as having a superficial and a deep layer, whereas I would prefer to describe it as a unit. Garrod (1876:340) listed species in which he believed the muscle was double while Gadow and Selenka (1891:243) pointed out that the tendency to have semi-separate layers is more marked in young birds.

Fisher encountered the two-parted condition of the pectoralis in the cathartid vultures (1946) and assumed (in conversation) that this represented an adaptation for soaring. He was much surprised at my report that this muscle did not have two parts in the eagles *Aquila chrysaëtos* and *Uroaëtus audax* although there was individual variation ranging from slight separation to distinct but incomplete separation. Fürbringer

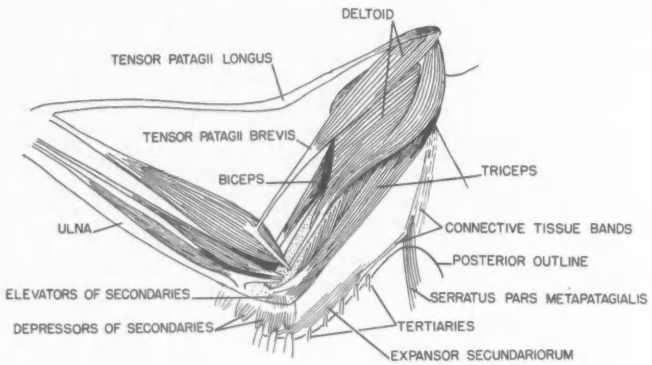

Fig. 2. Dorsal view of dissected wing of the Raven, *Corvus corax*; muscles overlying the scapula not shown.

(1888:422) reported the muscle of *Uroaëtus* and *Torgos* as double; my dissections of these genera do not support this conclusion. The problem here is to decide when this muscle is double. In my opinion it should be described as two parted only when there is total separation as in the cathartids or *Fregata*. To imply that it is double when in fact it is only partly so results in confusion.

A last example can be drawn from figure 33 in Hudson and Lanzillotti (1955) which shows the patagial fan of the Prairie Falcon (*Falco mexicanus*). In my dissections of the genus *Falco* and related genera I have never observed this style of fan. The difference is most likely due to the dissector. This same observation applies to some of the illustrations in Fürbringer (1888). The problem here is much like that of the metapatagium; in the separation of tendinous bands from the sheets of fascia, one really does not know where the one begins and the other leaves off; it is a matter of interpretation just how the fan should look. For a comparative study, it is necessary that all of the dissections be made by a single person. Otherwise the range of variation is greatly increased. Contrasting human and avian anatomy in this respect, it should be pointed out that the former is so well known that details can profitably be described; in the latter the general picture is still rather hazy.

In summary, I would stress the fact that certain aspects of avian anatomy are difficult to study and to interpret. What may be recorded in the literature as individual variation or specific variation may only be a matter of interpretation. This type of variation necessitates continual testing through parallel dissection until such time as our

knowledge is sufficient that we recognize significant and real differences when we encounter them.

The research for this commentary was a part of that directed toward the problem of the anatomy and phylogeny of the diurnal birds of prey. This project was supported by a National Science Foundation Grant (NSF G–1737).

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FROM FIELD AND STUDY

Communal Roosting of the Pygmy Nuthatch.—There has always been considerable speculation, especially among laymen, about where birds go at night. In the light of the following account, it seems a singular coincidence that Bent (U. S. Nat. Mus. Bull. 195, 1948:53) observed in his life history of the race *melanotis* of the Pygmy Nuthatch (*Sitta pygmaea*) that "very little is known about where and how birds spend their nights."

Some years ago Samuel W. Gadd, a journalist of Colorado Springs, Colorado, and an amateur ornithologist, told me of seeing a large number of Pygmy Nuthatches enter an old pine stub at dusk in the foothills just west of the Broadmoor section of Colorado Springs. I was unable to investigate this matter until early October of the following year at which time I found the location by following Gadd's directions. The tree in question was a very large yellow pine (*Pinus ponderosa*) which stood in the middle of a clearing. It had broken off about 30 feet from the ground, and the trunk which remained standing was pierced with holes. Subsequent investigation revealed it to be almost completely hollow, so that it consisted mainly of one very large cavity and a few additional minor cavities. As I sat at the edge of the clearing waiting for darkness, I heard the chattering of a flock of nuthatches approaching through the pines. It was apparent that the flock was quite large. Upon reaching the edge of the clearing, some individuals flew directly to the tree and entered the holes in the trunk. Others lingered in the surrounding pines investigating the bark and feeding. Eventually the remainder of the flock, individually and in small groups, flew to the old pine and disappeared into the holes. At first I tried to tally the incoming birds but lost count at 90. I finally estimated that there were at least 150 individuals roosting together in the trunk, with a minimum of 100 sharing the same cavity. Whether this large number of birds represented a single flock or a combination of several smaller flocks is unknown. The chattering continued for a short time, and then all was quiet. Before leaving, I tapped the trunk and was rewarded with more chattering but no birds flew out.

More recently Victor Favier, of the University of Colorado Biology Department, brought me the mummified remains of nine Pygmy Nuthatches he had found at the bottom of a cavity in a yellow pine stub in the foothills west of Boulder, Colorado. The plumages were in excellent condition and it was easily determined that the birds were all fully adult. Since then I have investigated seven other large dead yellow pine stubs in the same area. Six were empty but from a cavity in the seventh I recovered 13 dead Pygmy Nuthatches. The bodies, although desiccated and shriveled by the dry climate, were in a remarkable state of preservation. The plumages were nearly good enough for museum skins, and once again it was apparent that all the birds were adults. Both of the cavities containing dead nuthatches were large enough to have accommodated perhaps 40 to 60 birds and there was only one entrance hole at the top of each cavity which was deep and cylindrical.

Although these birds could have been overtaken by any one of a number of calamities, it is at least possible that they could have died of suffocation while roosting in large numbers in a poorly ventilated cavity. It also seems that this communal roosting behavior of large numbers of Pygmy Nuthatches is worthy of note. I have been unable to find reference to such roosting anywhere in the literature.—Owen A. Knorr, *Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, May 16, 1957.*

Southernmost Record of the Blue-winged Teal.—According to Hellmayr and Conover (Cat. Birds Amer., 13, pt. 1, no. 2, 1948:333–334) the southern limit of migration of the Blue-winged Teal (*Querquedula discors*), on the west coast of South America, is Lake Junín, Perú, northeast of the city of Lima, and on the east coast, French Guiana near Cayenne. On March 31, 1957, a specimen of *Querquedula discors* was taken in Uruguay, about 34° south latitude, near the Brazilian boundary and the Atlantic coast.

The region where the teal was obtained is extraordinarily rich in aquatic birds and migratory species, including plovers, terns, snipes, and birds of prey. Wintering ducks are abundant, especially the Cinnamon Teal (*Querquedula cyanoptera*) whose area of dispersal and migratory movements are still matters of discussion.

The record specimen, a male in breeding plumage, was collected by Mr. Enrique Gómez Haedo, in the Department of Rocha, within the extensive marshes adjacent to the "Parador La Coronilla."

The measurements are: wing 183 mm.; tail 67; culmen 41; tarsus 36.4; middle toe without claw 38.7. The skin is now deposited in the private collection of Rodolfo Escalante (Montevideo, Uruguay).

In view of the present record, the Blue-winged Teal may be added to the list of birds of Uruguay. Whether it is a regular or an accidental visitor is as yet uncertain, but this discovery marks the southern limits of migration as presently known.—Rodolfo Escalante and Enrique Gómez Haedo, *Montevideo, Uruguay, July 17, 1957.*

Fig. 1. Adult and two young of Galápagos Penguin at nest on Fernandina Island.

Nest of the Galápagos Penguin.—The nest of the Galápagos Penguin (*Spheniscus mendiculus*) has apparently not been reported previously. In the course of the Walt Disney photographic expedition to the Galápagos Islands, a nest of this bird was photographed on August 1, 1954, and it was observed on several later dates. The nest was located near Punta Espinosa, Fernandina Island, and it contained two downy young. The site was a rock cranny seven feet above high water. It was protected from direct sun by a lava slab, but aside from that it was an open and relatively exposed nesting site. On each of the five occasions that the nest was examined an adult bird was with the young.

There were many adult penguins in the area of Bolívar Canal at this time, and on several occasions groups of over 200 individuals were observed feeding in flocks with Brown Pelicans (*Pelecanus occidentalis*) and Noddy Terns (*Anoüs stolidus*).

In this area on Fernandina Island, adult penguins were often observed to disappear into deep lava cracks and potholes that extend for many yards into the jumbled rock piles of the shore. From deep holes of this kind, calls similar to those made by the nestling penguins were heard at several locations other than at the exposed nesting site. For this reason, and because no other exposed nests were found, I believe that the exposed site is less typical of the Galápagos Penguin than are the deeply hidden sites from which the calls of other nestlings were heard.—Jack C. Couffer, *Hollywood, California, July 29, 1957.*

Common Grackle in Utah.—On the morning of March 21, 1957, I collected a large icterid, later identified by Dr. C. Lynn Hayward as a Common Grackle (*Quiscalus quiscula versicolor*). It was collected from the higher branches of an apple tree on a farm located at 2470 West Street in West Provo, Utah County, Utah. This was the only grackle seen in the area. Other species observed in the immediate vicinity included the Brewer Blackbird.

According to William H. Behle, this appears to be the first record of this grackle in Utah confirmed by a specimen. The skin was deposited in the museum collection at Brigham Young University, Provo, Utah.—GEORGE M. TALLEY, *Zoology and Entomology Department, Brigham Young University, Provo, Utah, May 15, 1957.*

Cattle Egret in Costa Rica.—On December 3, 1954, and for three days thereafter, I observed a group of twelve Cattle Egrets (*Bubulcus ibis*) at Palo Verde, a cattle ranch located in the lower Tempisque Valley in the province of Guanacaste, Costa Rica. This is the first record for Costa Rica and apparently the first report of the species in Central America north of Panamá.

The birds had established temporary residence close to the hacienda's ranch house situated some 75 yards from the muddy edge of some deeply flooded fields. The cowboys, struck by the association between these little herons and cattle, claimed to have become aware of the birds only a short time before. It would seem, therefore, that the egrets had arrived at about the close of the rainy season. They were in their pure white winter plumage. The bill looked entirely yellow in some individuals but was orange-yellow in others; the legs were dusky (neither obviously blackish nor greenish).

Even aside from color characters the birds were distinctive. The bill, and also the neck, were relatively shorter than in similar species such as the Snowy Egret (*Leucophoyx thula*) and the Little Blue Heron (*Florida caerulea*). The feathering of the chin seemed to extend well toward the tip of the underside of the bill, giving the birds a puffy throated, almost goitrous, look which the Snowy and Little Blue lack. Perched, they always kept the neck drawn down into the hunched back; never was the neck held curved or even partially arched. Afoot, from a forwardly inclined stance, they would occasionally stretch out the neck horizontal to the ground, and they then exhibited peculiar, goose-like weaving motions. In flight, the wings were beaten more rapidly than in the other small herons, and the general appearance in the air was more gull-like than heron-like. Except when spreading out to feed, the birds kept together as a unit when at rest or in flight. They settled on trees or, more often, rested individually upon a row of half-drowned fence posts. As regards voice, during the several days on which they were observed the birds uttered rarely only a low *kruk* which was quite different from the lengthened, guttural croaks of other small herons.

When feeding, the Cattle Egrets alighted beside livestock. Indiscriminately they transferred their attentions from cattle to horses and pigs, and also from certain individuals to others. They attended the animals favored at the moment in the ratio of either one bird to one beast or of several to one. With the neck extended, they looked up in an inquiring manner at the grazing horses and cattle, or down at a mired pig. The egrets might move up close in order to pluck a parasite from an animal's hide, or seize an insect stirred up in the grass. The livestock appeared oblivious to the birds' existence. When the host beasts moved onward, the birds hurried after them with an odd neck-flopping. Whereas other small herons regularly retract the neck or bob the head at each step, the Cattle Egrets extended the neck like a goose, a few steps being required for the body to catch up with the head. Among the species known to me this gait most resembled that of a Sun-Bittern (*Eurypyga helias*). From time to time a Little Blue Heron would join the Cattle Egrets, not to follow the cows but, possibly, out of curiosity or perhaps for company's sake. The egrets disregarded the visitor, which would fly away after a short time.—PAUL SLUD, *University of Michigan Museum of Zoology, Ann Arbor, Michigan, May 2, 1957.*

Black Swan in Kelp off Southern California.—About midday on May 24, Earle G. Cunnison and I flushed an adult Black Swan (*Chenopis atrata*) as we approached the kelp bed off Torrey Pines, San Diego, California. At the time we were in a small boat about 300 yards off shore. The swan rose about 75 yards ahead of us, flew westward, then circled southward, remaining over the sea at a height of less than 50 yards. Grinnell and Miller (Pac. Coast Avif. No. 27, 1944:559) reported that the Black

Swan is "sometimes seen out of captivity on lowland bodies of water in company of wild waterfowl." The bird we saw was alone.

In its native Australia the Black Swan is most abundant in fresh water, but at times it is common on salt water, particularly in lagoons and on tidal flats. It generally avoids open, rough water, moving as the wind changes to feed in the lee of a bank or point (Mathews, The Birds of Australia, 4, pt. 1, 1914–1915:12–22, pl. 200). The habitat where the bird reported here was observed therefore seems unusual. Inquiry at the San Diego Zoological Garden and from a local bird fancier who keeps Black Swans has failed to indicate that any birds of this species have been lost recently.—JAMES R. STEWART, *Scripps Institution of Oceanography, University of California, La Jolla, California, June 13, 1957.*

Pigeon Wing-beats Synchronized with Breathing.—Moving pictures of a pigeon (*Columba livia*) in flight reveals that it inhales on the upstroke of the wings and exhales on the downstroke. The analysis of breathing was aided by fastening a rubber balloon over the bill and external nares of the bird, leaving a small area at the rear of the mouth uncovered for an air passage. As the bird breathed, the balloon collapsed and expanded. The balloon was left in place for over an hour, and the bird showed no signs of distress. The bird was an adult homing pigeon flying free except for a long light line secured to a light harness which did not apparently interfere with normal flight. The tether kept the pigeon within range of a 16mm. camera. Thirteen complete wing-beat cycles at 48 frames per second were carefully analyzed with the results stated above, and six more cycles at 32 frames per second agreed with these results, although they were not as complete. The pigeon was photographed in short flights of about 30 feet. The method works very well and should be adaptable to other types of birds under different conditions.

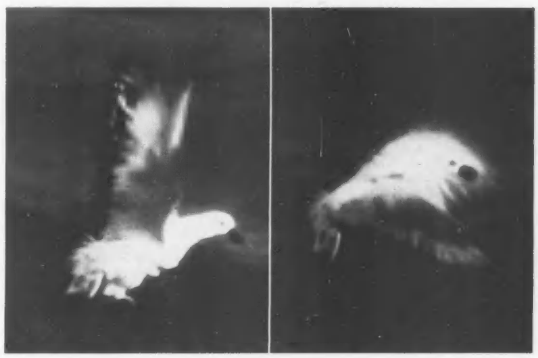

Fig. 1. Flying pigeon with balloon on bill. Left, upstroke, showing collapsed balloon. Right, start of upstroke with balloon inflated.

The figure shows on the left a pigeon near the end of an upstroke with the balloon collapsed and, on the right, the start of an upstroke with the balloon still expanded from the preceding downstroke. The inhalation begins at this position. These illustrations are copied from 16mm. Kodachrome film. A red balloon was used. The collapsed state of the balloon could be readily detected on the film by shadows along the sides of the open mouth. Unfortunately these shadows do not show in these reproductions. It is suggested that white or yellow balloons be used for better photographic recording in future tests.—JACK T. TOMLINSON, *San Francisco State College, California,* and ROBERT S. MCKINNON, *Oakland Junior College, Oakland, California, July 1, 1957.*

A Western Representative of the Rufous-sided Towhee Collected in New Jersey.—On December 23, 1952, while on the Raritan Estuary Christmas Census, Mr. George L. Daniels and I were canvassing a swamp located near Metuchen, Middlesex County, New Jersey. In the process of counting the various birds present, my attention was drawn to an unusual towhee which hopped out

of a nearby brush pile. The next day at dawn I was again at the scene and was able to collect the bird. The specimen, a female, was examined by H. C. Oberholser and Allan J. Duvall and identified as *Pipilo erythrophthalmus montanus*. It appears that this is the first record of this subspecies east of the Mississippi River. The bird was given to the Fish and Wildlife Service and is now no. 421001 in that collection.—JAMES BAIRD, *Norman Bird Sanctuary, Middletown, Rhode Island, June 9, 1957.*

Pale Ouzel Nesting in Korea.—On May 25, 1957, in a grove of small cryptomeria trees approximately five miles north of the city of Pusan, Kyongsang Namdo, Korea, a female Pale Ouzel (*Turdus pallidus*) flushed from a nest in a tree directly over my head. The grove was located on artificially terraced, reforested mountain slopes surrounding a reservoir. The elevation was estimated as approximately 800 feet. The slope was grassy and swampy, and most of the trees ranged from 25 to 30 feet in height and were about six inches in diameter.

The nest was located on a small, heavily-foliaged, horizontal branch close to the trunk of the cryptomeria tree, approximately 15 feet above the ground. It was constructed of coarse dry grass and mud. The cup was lined with rootlets, dry green moss, and several dry, partly decomposed deciduous leaves. The nest measured in outside diameter 12.5×13.0 cm. and was 7.5 cm. in overall height. The inside diameter was 7×8 cm. across the top and was 5 cm. in depth. The nest contained four young with eyes still closed, probably two to three days of age.

The female flushed with considerable wing noise, flew to another cryptomeria about ten feet distant, and voiced apparent concern at my presence with frequent sharp "scolding" notes of a typical thrush-like quality. As I backed away to collect the bird, it followed me at a distance of 10 to 15 feet. The skin was deposited in the Museum of Vertebrate Zoology.

The adult male was neither seen nor heard during the 45-minute period I spent in the vicinity of the nest. As far as I am able to ascertain, this is the first nesting record of this species in Korea.—CHESTER M. FENNELL, *Seoul, Korea, July 16, 1957.*

Another Record of the Shearwater Puffinus puffinus newelli.—Richardson (Auk, 72. 1955:412) recorded a recently dead example of *Puffinus puffinus newelli* which flew into the room of a building on the Island of Oahu and survived for a short time at the Honolulu Zoo. According to Murphy (Amer. Mus. Novit., no. 1586, 1952:11), there were seven previous records of this race of the Manx Shearwater, but only two specimens had been preserved. The specimen recorded by Richardson apparently, therefore, represented an eighth record and a third specimen.

A ninth record and a fourth specimen seem worth noting. An adult male shearwater of this form was found at Koloa, Kauai Island, on October 8, 1956, and died shortly after arrival at the Honolulu Zoo. The specimen was made up by George C. Munro and presented to the Yale Peabody Museum. A few notes on color by Mr. Munro may be worth recording: "iris, bright reddish brown; bill black, lower part of mandible lighter, with a bluish tinge; legs a fleshy bluish gray color" with the exception of the following parts which were black: outer toe, part way up outer part of leg, outer part of second toe, and claws. In addition, Mr. Munro notes that the sternum measured three and one-half inches in length and that the bird was fully mature, very fat, and seemed if anything rather old; the testes were very small.

In this specimen the under tail coverts are entirely white, the sides of the lower neck and breast are blackish, and the area immediately below the eyes is neatly banded with alternate black and white feathers that give a mottled effect. The specimen measures: wing (worn) 224 mm., tail (worn) 85, culmen 33.5, and tarsus 47.5.—S. DILLON RIPLEY, *Peabody Museum, Yale University, New Haven, Connecticut, June 11, 1957.*

NOTES AND NEWS

The National Science Foundation will award grants to defray partial travel expenses for a limited number of American scientists who wish to participate in the XIIth International Ornithological Congress which is scheduled to meet in Helsinki, Finland, June 5 to 12, 1958.

Application blanks may be obtained from the National Science Foundation, Washington 25, D.C. Completed application forms must be submitted to the Foundation by January 20, 1958.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the life sciences is January 15, 1958. Proposals received prior to that date will be reviewed at the winter meetings of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the January 15, 1958, closing date will be reviewed following the spring closing date of May 15, 1958.

Inquiries should be addressed to National Science Foundation, Washington 25, D.C.

The annual index for The Condor for 1957 was prepared by Mrs. Sylvia L. Thomssen, to whom members are much indebted for this valuable aid.

PUBLICATIONS REVIEWED

AUDUBON WESTERN BIRD GUIDE. By Richard H. Pough. Doubleday and Company, Garden City, New York, xxxvi+316 pp. June, 1957. $4.95.

To design and prepare a bird guide that is at once useful and authoritative is a difficult task. The requirement of compactness competes with adequate coverage of fauna and natural history. The writing must also reflect not merely sound compilation but intimate acquaintance with species. It was the latter attribute that made the earlier Hoffmann manual so extremely valuable. The new Pough guide, within the limits set for it, is well executed, both in writing and illustration. Where it falls far short of adequacy is in plan, for in effect the book is the tag-end of a series of manuals and in no sense provides a complete coverage of the western species. This is evident from the following considerations. Only those species are treated fully that were not represented in the Audubon Water Bird Guide or in the Audubon Bird Guide, which latter dealt with small land birds of central and eastern North America. The author states that there are 614 species of western North American birds, but of these only 203 are given coverage on the subjects of identification, habits, voice, and nesting. Thus a student of western birds will not be served properly unless he has all three guides at hand and is prepared to jump back and forth between them, using the cross references in the western unit. The 411 species that are not covered fully are merely entered with a condensed statement of range, although quite a few of them are represented by additional illustrations in the Western Guide. Incongruous situations thus arise such as limited treatment of the characteristically western Verdin, Sooty Shearwater, and Bewick Wren whereas there are full accounts of such inconsequential vagrants as the Wryneck, Black-tailed Gull, and Mountain Accentor.

There are 340 illustrations in color by Don R. Eckelberry. This skilled artist has done his usual fine work, although hampered by the requirement of severely crowding all of these on to 32 color plates grouped in the center of the book. The 138 black and white illustrations by Terry M. Shortt are chiefly of birds in flight and are arranged conveniently in the text. Most of these are good; only occasionally do they seem to fall short of reality, and all are helpful.

Pough sought aid in writing from Howard C. Cogswell, Joe T. Marshall, Jr., Robert W. Storer, and Allan R. Phillips. These authors, whose species accounts are initialed, cover approximately a third of the 203 forms given detailed treatment, the greatest number being contributed by the first two persons. All their statements reflect intimate acquaintance with the species they report on and their own special interests in phases of the birds' natural history.

The guide benefits from having available the scientific and vernacular nomenclature of the new 5th edition of the A.O.U. Check-list. It wisely deals with species almost solely, and only rarely, and usually justifiably, refers to a few well-marked races.

In summary, we state our regret that the plan of the Audubon guides, rigidly pursued, has led to this third volume on western birds which is far from ideal in its conception and coverage. Indeed the book will prove rather exasperating, for one must use it in part for its values of written statement and illustration and yet can not really employ it or recommend it as an effective western guide.—ALDEN H. MILLER.

COOPER SOCIETY MEETINGS

NORTHERN DIVISION

FEBRUARY.—The monthly meeting of the Northern Division of the Cooper Ornithological Society was held on February 7, 1957, at the University of California, Berkeley. The following names were proposed for membership: Mr. Raymond R. Johnson, 410 Fairmont Avenue, Oakland, Calif., by Alden H. Miller, and Robert S. Hoffmann, Department of Zoology, Montana State University, Missoula, Mont., by Frank A. Pitelka.

Donald McLean reported that a male European Widgeon was seen on January 26 on a small pond east of King City in Monterey County. Paul Covel said that a Barrow Golden-eye was seen on Lake Merritt, Oakland, from January 10 to 17.

Mr. Carol Ferrel presented a talk entitled: "Federal Aid and its Part in California Wild Life Management."—HARRIET P. THOMAS, *Acting Secretary*.

APRIL.—The monthly meeting of the Northern Division of the Cooper Ornithological Society was held on April 4, 1957, at the University of California, Berkeley. Minutes of the previous meeting were read and approved. The following names were proposed for membership: Jane Roberts Durham, 968 Cragmont Avenue, Berkeley 8, Calif., by Alden H. Miller, and Charles S. Thaeler, Jr., 2214 Haste St., Berkeley 4, Calif., by Frank A. Pitelka.

Dr. Miller announced that he had received a letter from Frank Richardson of the University of Washington stating that someone had broken in and stolen their mounted specimen of the Whooping Crane. Jack Guggolz and Laurence Curl reported seeing a Baltimore Oriole in Albany, California, recently. Donald McLean reported two adult Harris Sparrows approximately two weeks ago near Paso Robles, California.

Dr. Miller commented on the range extension of the Chestnut-backed Chickadee; the species was seen on March 23 in the cyprus trees along the rodeo grounds at Salinas. Florence Plymel reported a Barrow Golden-eye on March 10, 15, 17, and 20 at Palo Alto Yacht Harbor.

John Davis, speaker of the evening, discussed "Winter Invasion of the Clark Nutcracker in the Lowlands."—LILLIAN K. HENNINGSEN, *Secretary*.

MAY.—The monthly meeting of the Northern Division of the Cooper Ornithological Society was held on May 2, 1957, at the University of California, Berkeley. The following name was proposed for membership: Harold G. Peterson, 3548 65th Ave., Oakland 5, a joint member of the Cooper Society and Western Bird-Banding Association, by Junea W. Kelly.

President McLean said that he was in the Imperial Valley in the Colorado River area in the preceding week just in time to witness the arrival of the White-winged Doves which apparently came in during the night. On Tuesday he saw none; on Wednesday he saw one; and by Thursday there were doves calling everywhere at daylight.

Lee Merriam Talbot gave an illustrated talk on "The Spectacular Serengeti, a review of Africa's Plains wildlife migration."—HARRIET P. THOMAS, *Secretary, pro tem*.

SOUTHERN DIVISION

MAY.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on May 28, 1957, at the Los Angeles County Museum. The following names were proposed for membership: James M. Gates, 421 N. Euclid Ave., Tucson, Ariz., by Allan R. Phillips; Ronald E. Langston, 48 Kirkwood Lane, Greenville, S.C., by Jack C. von Bloeker, Jr.; Stanley B. Mulaik, Zool. Dept. Univ. Utah, Salt Lake 12, Utah, by Mrs. Fern Taintor; Lawrence Kilham, 7815 Aberdeen Rd., Bethesda 14, Md., and Joseph F. Mount, 10770½ Strathmore Dr., Los Angeles 24, Calif., by T. R. Howell; Mrs. Alice G. Gray, 6645 Heartwood Dr., Oakland 11, Calif., and Dr. D. M. Whitelaw, 5760 Marguerite St., Vancouver, B.C., by F. H. Boynton; Roland H. Wauer, 230 So. 8th St., San Jose, Calif., by F. R. Mewaldt; Ruth M. Smith, 1217 Cypress Ave., Santa Ana, Calif., by E. N. Harrison; Lawrence M. Bartlett, Dept. Zool., Univ. Mass., Amherst, Mass., Edward W. Beals, Dept. Botany, Univ. Wisconsin, Madison 6, Wis., Reed W. Fautin, Dept. Zoology and Physiology, Univ. Wyoming, Laramie, Wyo., James M. Hartshorne, 108 Kay St., Ithaca, N.Y., Mary Lewis, 925 Dauphine, New Orleans 16, La., Henry Milton Reeves, P. O. Box 1786, Harlingen, Tex., Stephen M. Russell, Mus. Zool., Louisiana State University, Baton Rouge, La., Mrs. Ruth E. W. Wheeler, 3 W. Carrillo St., Santa Barbara, Calif., and James R. Youse, Lava Beds National Monument, Tulelake, Calif., by C. V. Duff.

Mr. John B. Davidson, speaker of the evening, chose as his subject, "Australian Walkabout."—DOROTHY E. GRONER, *Secretary*.

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